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Technical Report 50

THE BIOLOGY AND ECOLOGY OF *PASSIFLORA MOLLISSIMA* IN HAWAII

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March 1984

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NATIONAL PARK SERVICE Cooperative Agreement No. CX8000 2 0001

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ABSTRACT

Passiflora mollissima (HBK.) Bailey, a perrenial climber from the Andean highlands, is currently proliferating in koa (Acacia koa) and 'ohi'a (Metrosideros collina) forests on the islands of Hawai'i and Kaua'i. Since its introduction to the islands in the early part of this century it has spread rapidly and now occupies nearly 500 km2. Infestations range from scattered individuals with low cover to complete dominance of an area, inhibiting the growth and reproduction of forest trees.

This vine, commonly known in Hawai'i as "banana poka" has been variously referred to as Passiflora mollissima or P. mixta or as the product of introgressive hybridization between P. mollissima and an unknown species. Quantitative and qualitative characters were evaluated in an attempt to characterize the Hawaiian taxon. Comparison of these data with the most recent taxonomic treatment of Passiflora showed that most characters are within the range of those of P. mollissima. It is concluded that the Hawaiian taxon should be considered Passiflora mollissima sensu lato. Brief mention is made of the similarity between the Hawaiian population and several populations in other Pacific areas.

The ecology and life history of P. mollissima were studied in three areas on the island of Hawai'i. In this species, seeds require a short period of afterripening. Germination is staggered and most seedlings emerge within 4 to 12 weeks. Germination success is not affected by light intensity but the rate increases with increasing light and associated higher temperatures. At very low light intensites (2.0% RLI) the germination rate is significantly inhibited. Ingestion of seeds by feral pigs has little effect on germination; they function principally as effective, short-distance dispersal agents.

Densities of germinants ranged from 640 to 554,000 indiv./ha. and were considerably higher in areas of heavy pig activity. Growth of seedlings is slow compared with other stages in the life cycle. Heaviest mortality occurs between the germinant and seedling stage. The juvenile phase is characterized by rapid growth rates (up to 3 m/yr) and a distinctive morphology which is also found in rapidly-growing (flushing) adult shoots. Survival from the juvenile to the adult phase of the life cycle is very high. Under favorable conditions, individuals may go from seed to reproductive maturity in a single year. All populations sampled were stable and reproducing.

The reproductive pattern of P. mollissima promotes both allogamy and autogamy although selfing is favored. A high degree of self- compatibility is indicated, although autogamy occurs in low frequency in the absence of pollinators, which are principally exotic insects. Pollinator efficiency is quite low,

however (30%). Passiflora mollissima exhibits continuous growth and reproduction in Hawai'i; both individuals and populations are asynchronous. Seasonal differences in behavior are reflected in the relative magnitude of activity throughout the year. Peak activity of reproductive phases tends to be concentrated into a single annual period while growth is less seasonal. All phases of flowering are concentrated in the drier summer months (May-Aug.), fruiting in the wet winter months (Dec.-Mar.). No strong correlations were found between climatic variables and phenological activity, however.

The relative shade tolerance of P. mollissima and its mode of establishment in closed-canopy forests of Hawai'i was studied using a series of shade levels under both natural and artificial conditions. Net assimilation rates and relative growth rates increase with increasing light intensity. Optimal growth occurs in full sun (100% RLI). Intermediate levels of shade (2-14% RLI) induce etiolation and result in rapid height growth. Greatest shade tolerance is exhibited at these intermediate intensities. At very low light levels (0.35% RLI) growth is severely restricted and some individuals are regularly below the compensation point.

As growth is proportional to light intensity, the magnitude of a disturbance, or gap size, has a direct effect on the rate and pattern of establishment. Following a disturbance, increases in cover and biomass of P. mollissima are proportional to levels of canopy disturbance and associated higher light intensities. Density is not proportional to the amount of biomass and cover present. The rapid and synchronous colonization of plots under conditions of 100% canopy removal also suggests that disturbance stimulates the germination of seeds present in the soil. From these data it is concluded that although closed-canopy forests in Hawai'i are not optimal habitats they are nonetheless susceptible to invasion and infestation by this exotic vine, following regular canopy disturbance.

CHAPTER ONE

LITERATURE REVIEW

INTRODUCTION

Several studies of native Hawaiian rain forest communities (Mueller-Dombois et al. 1981; Burton and Mueller-Dombois in press) have shown that their character differs from those in the vast Indo-Malaysian and South American rain forest belt (Richards 1952; Whitmore 1975). The relative isolation of the islands has resulted in a number of floristic gaps (Carlquist 1980). Forests in Hawai'i have a lower species diversity when compared with continental associations. A common life form which is poorly represented is the climbers, particularly lianas or woody vines. Though several examples of large native climbers are found in upland forested areas--e.g., Freycinetia arborea Gaud. ('ie'ie), Alyxia olivaeformis Gaud. (maile), Smilax sandwicensis Kunth. (hoi-kuahiwi), Ipomea congesta (Burm.) Merr. (koali-'awania)--they are seldom seen proliferating in the upper canopy layers, ususally comprising less than one percent of the total ground cover (Mueller-Dombois et al. 1981). Some introduced climbers, particularly the aroids, Scindapsus spp. and Philodendron spp., are frequent in exotic forest plantations but do not successfully invade nearby native forests. Other exotics--e.g., Passiflora edulis Sims. (liliko'i), P. ligularis Juss. (lemi-wai), Paederia foetida L. (maile-ka-kahiki)--are found in abundance in some disturbed upland areas, but no other woody vine can be found in the forest today in such abundance and vigor as the aggressive exotic, Passiflora mollissima (HBK.) Bailey.

Passiflora mollissima, known locally as banana poka, is proliferating in mid and high elevation forests on the islands of Hawai'i and Kaua'i. From the centers of introduction by man, populations are continuously extending their range, aided principally by feral pigs, (Sus scrofa L.), the chief dispersal agent in Hawai'i (Wong 1971a; Giffin 1972; Baker 1975). Infestations range from few individuals with small cover, in the 'Ola'a Rain Forest, to essentially pure stands, comprising a majority of the biomass and nearly one hundred percent cover in the Laupahoehoe section of the Hilo Forest Reserve. These latter infestations have resulted in declining stands of native 'ohi'a-koa (Metrosideros collina (J. R. and G. Forst.) Gray--Acacia koa Gray) forests and little reproduction of all canopy tree species. The necessity for control of this aggressive species has been recognized by federal and state agencies (Tagawa 1972; Wong 1973; Tamura 1978a; Anonymous 1979; Skolmen 1979).

The following paper reviews the role of vines in tropical forest ecosystems and the autecology of P. mollissima in its

native range (South America) and areas where it has been introduced as an ornamental or a fruit crop. The literature pertaining to this species in Hawai'i is reviewed separately.

THE ROLE OF LIANAS IN TROPICAL FOREST ECOSYSTEMS

> "We stand wonderstruck and helpless; without a man-made path there is no access into the forest. Its margin is like a wall bound by lianas in all direction, and covered with leaves of every possible hues of green. Natives are sent ahead to cut a path with handy heavy-bladed knifes called machetes, while we rest in the shade. The lianas are most impressive, some thin as a pencil, some woody and thick as a man's waist, hundreds of meters long, entwining the trees in countless, irregular coils in search of light in the canopy of leaves." (Raciborski 1924, in Szafer 1975)

One of the most striking features of the lowland tropical rain forest is the abundance and immensity of climbing plants found therein. The climbing habit has evolved repeatedly in diverse taxa of the plant kingdom; nearly fifty percent of all higher plant families contain climbers (Schenck 1892, in Richards 1952). Families containing a large percentage of vines, such as the Apocynaceae, Bignoniaceae, Leguminosae, Menispermaceae, Passifloraceae and Rubiaceae, are often principally tropical in distribution. In reviewing the taxonomic distribution of climbing species, Penalosa (1976) noted that some families predominantly contain climbing genera, suggesting that the "development of the habit phylogenetically preceded generic evolution." Other families are composed of relatively few climbing genera and species, denoting generic evolution prior to the appearance of scandent members. The occurrence of erect members in an otherwise climbing taxa was interpreted by Schenck (1892, in Richards 1952) as representing, in those species, a loss of the ability to climb. These aspects of the taxonomy of climbing species indicate that the evolution of the climbing habit is an ancient yet ongoing phenomenon.

Although not always clearly differentiated, two major ecological groups of climbers may be delimited by the strata in which they mature and their photosynthetic strategies (Richards 1952; Grubb et al. 1963). Understory or skiophytic (shade plants) climbers, often have small, herbaceous stems and climb by means of modified roots. No distinct crown is formed, rather, leaves are produced along the trunk of the host tree. Heterophylly is a common feature of many members. Lianas (woody climbers) may also be restricted to the understory. Shade tolerant at maturity, skiophytes remain in the understory and play a very minor role in the structure and economy of the community (Richards 1952; Grubb et al. 1963; Madison 1977). Typical members include many of the pteridophyte climbers and the monocotyledons, particularly the Araceae.

In contrast, the photophytic (sun plant) climbers are more often woody. Although they may be shade tolerant as juveniles, adults typically are found in the full sun of the upper canopy layers or forest openings where they form a distinct crown. Lianas tend to exhibit greater morphological specializations, including the development of tendrils. This highly evolved organ allows for an even greater economy of stem material, by supporting the liana stem, and individuals often climb to great heights. Some photophytic climbers are important structural components of mature undisturbed forests; others are more characteristic of secondary growth forests. The remainder of this section will principally review the literature pertaining to woody, photophytic climbers.

Morphological and Physiological Adaptations of Lianas

The architecture of lianas is uniquely structured to meet the demands of their particular habit. Little biomass is allocated to supporting tissues. The use of a host tree for mechanical support has allowed lianas to exploit the greater light intensities found in the upper canopy. Commonly a single unbranched stem ascends into the canopy (Jones and Gray 1977). The cable-like construction of stems, characterized by scattered vascular bundles surrounded by thin-walled storage parenchyma or anomalous secondary growth patterns in which thick-walled fibers and tracheary elements are embedded in thin-walled cells, provides flexibility with considerable tensile strength (Richards 1952; Esau 1977). The copious amount of storage parenchyma in stems allows for longevity (Richards 1952). These distinctive anatomies may represent gross structural changes, but often adaptations are simply quantitative changes from one of the basic types of architecture found in trees (Halle et al. 1978). Although other life forms, such as epiphytes, hemi-epiphytes and stranglers employ similar "strategies" of mechanical dependence, none have been as successful as lianas (Richards 1952).

Lianas generally proliferate following disturbance, increasing in abundance, vigor, leaf area and biomass with increasing light intensities (Richards 1952; Fogge 1960; Jones and Gray 1977); this response may be considered an expression of heliophily (love of the sun). Calculated growth rates and the scarcity of individuals in intermediate height classes indicate that lianas quickly reach the canopy, where increased irradiances stimulate profuse branching and reproduction (Richards 1952; Brender 1961; Janzen 1971; Choudhury 1972). Many lianas appear unable to flower unless subjected to high light intensities (Richards 1952; Penfound 1966; Breteler 1973).

The positioning of a majority of the transpiring phytomass in the relatively arid conditions of the upper canopy necessitates the transport of large volumes of water through disproportionately slender stems (Janzen 1974; Croat 1975). In the predominantly climbing Passifloraceae, Ayensu and Stern (1964) and Carlquist (1975) found that scandent members possess

specializations--e.g. wider vessel diameters, simple perforation plates, and a high proportion of conducting to supporting fibers--which reduce xylem resistances, thereby allowing accelerated rates of upward water and solute translocation.

Dimorphism and the Evolution of the Climbing Habit

The classification of a particular taxon as a tree, shrub or vine in some cases reflects a characteristic morphology which is observable in most members; in others, it merely reveals man's continual inability to create absolute categories into which all of nature can fit. There exist many transitional stages between "true lianas" and independent plants, including weak-stemmed trees, scandent shrubs and hemi-epiphytes (Richards 1952). In some climbers, the habit is facultative and the same species may have several growth forms (Halle et al. 1978).

In searching historical and contemporary literature in botany and horticulture, one may find the same taxon variously described by different authors: different terminologies are often used by explorers, botanists and horticulturalists to describe taxa and record observations. The following example illustrates this point: Podranea brycei (N.E.Br.) Sprague, a woody plant from South Africa, has been variously described as a subshrub, shrub, scandent undershrub, climbing shrub, showy climber and small tree (Menninger 1970), suggesting that it is an extremely plastic species.

In his review of the literature on climbing plants, Penalosa (1976) notes that complex growth patterns commonly occur in vines. For skiophytic climbers, this is usually manifested as heterophylly but may be accompanied by changes in stem morphology (Strong and Ray 1975; Madison 1977). In contrast, shoot polymorphism is more prevalent in photophytic climbers and references to heterophylly are less common (Jacobs 1976).

Most examples of complex growth deal with changes in form from a climber to a shrub, or the reverse, rather than differences in anatomy or morphology of the shoots themselves. With few exceptions discussions are based upon observation rather than experimentation. Jacobs (1976) however, notes that some lianas which have a suffrutescent form exhibit a vascular anatomy comparable to erect life forms rather than the interrupted vascular cylinder characteristic of climbers.

Several authors have remarked that young plants of climbing species tend to remain shrubby in open, well-lit areas in the absence of supporting trees; these individuals may reach maturity and flower in this condition. In shaded habitats, the climbing form prevails (Richards 1952; Menninger 1970; Walter 1971). For example, Mussaenda erythrophylla Schum. and Thonn., commonly cultivated as a shrub, becomes scandent if light is limiting (Menninger 1970). The relationship between high light intensity

and suffrutescent growth does not hold true for all species examined. In climbing members of the Dichapetalaceae, seedlings which germinate in the shade produce shrubby individuals; scandent shoots are produced at higher light intensities (Breteler 1973).

Light alone may control the ultimate growth form of lianas, but it is more probable that a complex of factors associated with high light intensities is responsible. Principal among these is plant water relations. Depending upon the size of openings involved, well-lit areas may be much drier than surrounding forests. The correlation of high light intensity with drought conditions is well-established, as is the predominance of chamaephytes in drier habitats--e.g. the mediterranean scrub association--(Daubenmire 1974; Szafer 1975). Observations by Jacobs (1976) that the shrub stage of growth is retained by certain climbers under drier conditions, support this assumption. In the predominantly climbing tropical family Dichapetelaceae, the only non-climbing species are those found in arid areas (Breteler 1973). The persistence of the shrub habit under high light intensities or water stress may constitute a direct physiological response to changes in environmental conditions; fast-growing, climbing shoots may not be produced when the absolute growth rate falls below a critical level.

Several authors consider the existence of two growth habits in lianas indicative of a discrete juvenile phase in the life cycle which is characterized by differences in morphology and physiology (Robbins 1957; Cremers 1973, 1974; Greulach 1973). These studies employed experimental methods rather than observation alone, but are few in number. In the English Ivy (Hedera helix L.), a temperate woody vine, juvenile plants have flexible, trailing stems, palmate leaves and are purely vegetative. The adult stage, occurring infrequently, has a shrubby appearance with rigid, woody stems and ovate leaves and normally produces abundant flowering shoots (Robbins 1957; Greulach 1973). These changes are controlled by gibberellins. In these studies, juvenile grafts produced only juvenile shoots while adults produced mature branches. Spontaneous reversion to the juvenile state was rare.

A more comprehensive study of vine architecture was carried out by Cremers (1973,1974). Twenty species of African rain forest lianas were grown from seed and their growth patterns recorded. Results showed the existence of two distinct growth phases in the climbers examined. Juveniles were non-climbing and sterile; adults climbing and reproductive. These stages could be distinguished by differences in growth rate, leaf size and shape, internode length and reproductive capacity. The decision as to whether these conclusions are generally applicable to lianas must await further comprehensive studies of this sort.

Complex growth in vines may simply be an expression of paedomorphosis but in many cases appears to be a more complex

phenomenon. The shrub phase of climbing species may represent a genetically controlled adaptation to a varying environment or be interpreted as the retention of a stage in its evolutionary history.

Before leaving the subject of complex growth forms, it should be noted that an abrupt change in form with age, known as habit-heteroblastism, occurs in a small group of New Zealand trees and shrubs. Plants begin life as shrubs and at a particular point in time, from several years to decades later depending on the species, become arborescent. In this same manner, trees may also become suffrutescent with increasing age (Philipson 1963). This phenomenon parallels the shoot-polymorphism of vines in several notable ways:

1. These phenomena are not restricted taxonomically but occur in a variety of plant families.
2. Endogenous as well as exogenous factors are believed to be involved.
3. Changes in shoot morphologies are sometimes, though not always, accompanied by heterophylly.
4. Plants with "juvenile" morphologies may be reproductive.
5. The shrub life form is found both in well-lit and shaded habitats.
6. Morphological differences may be accompanied by changes in anatomical features, particularly in the xylem.

Distribution

In one of the earliest and most comprehensive works on vines, Schenck (1892, in Richards 1952) noted that although climbers are a feature of most plant communities where supporting trees are found, nearly ninety percent of all climbing species occur in the warm, humid tropics. Putz (1982), noted however that the species richness of all plants is generally greater in tropical areas, suggesting that the percentage of climbing species may not be excessively high.

In an attempt to explain the distribution of climbers, several authors concluded that the strategy of heliophytic lianas creates problems of water stress, thus limiting their distribution to humid environments (Richards 1952; Gessner 1956; Croat 1975). A different approach to the problem led Janzen (1974) to conclude that nutrient poor soils determine the distribution of vines. He states:

> "The success of the vine life form clearly depends on its ability to grow rapidly in length. The biomass of vines is disproportionately reduced in tropical habitats where the absolute growth rate is reduced for all plants, such as at elevations above about 2000 to 2500 m, and in deserts."

Janzen's conclusions are drawn from his review of productivity on

white sand soils in tropical regions. Classified as podsols or spodosols, these soils are characteristically highly leached, nutrient poor soils with low productivity (Brady 1974) and notable in the absence of fast-growing life forms such as lianas and annuals (Janzen 1974). In these habitats, lianas are scarce at forest edges and clearings, where they typically show their greatest concentrations. Richards (1952) also noted the general absence of lianas in the coarse white sand soils of Guiana but attributed this to the vines' inability to tolerate the excessive rates of evaporation in the understory. The paucity of climbers in white sand caatinga vegetation of Venezuela (Putz in press) further supports Janzen's hypothesis.

In still other cases, efficient rates of water conduction allow vines to prevail in drier, more seasonal habitats. In his work on the distribution of the Bignoniaceae in Tropical America, Gentry (1976) found that the absolute density of vines was greater in drier environments. These results agree with the conclusions of Holdridge et al. (1976), also working in Tropical America, who pointed out that lianas were most abundant and conspicuous in semi-deciduous lowland forests.

The Ecological Role of Lianas in Tropical Forest Ecosystems

Primary Forests

Tropical rain forests exhibit a high degree of structural diversity. The dense, multi-layered canopies characteristic of most lowland tropical rain forests are largely an expression of the intense competition for a limited amount of light. In reviewing the light regimes of tropical forests, Burton (1980a) noted that irradiances measured on forest floors averaged only 1.5 percent of those under similar open conditions. Whereas evolution has favored the development of the arborescent habit, evidenced by the dominance of trees in these environments, the climbing habit evolved as a highly competitive adaptation. Although adult lianas are fewer in number than trees, they play an essential role in the structure and integrity of the climax forest community.

According to Richards (1952), "in undisturbed rain forest of normal density, lianes, though always present, are never exceedingly common. They only become abundant enough to impede progress in well-lit places." However, in a seasonally dry, semideciduous monsoon forest in Asia, climbers comprised approximately ten percent of the total forest biomass and nearly forty percent of the total measured leaf biomass, significantly affecting primary productivity in the area (Ogawa et al. 1965 a,b). In a tropical rain forest on nutrient poor soil in Venezuela, Putz (in press) found that lianas comprised only four percent of the total above-ground biomass (15.7 tons/hectare) but 20 percent of the total leaf area. Lianas may also significantly contribute to the species richness of tropical forests, constituting twenty percent of the species present in a given area (Penalosa 1976).

Vines occur in all stages of forest succession, but often the same species does not regularly occupy more than one stage of succession (Liew 1973a,b; Budowski 1965; Benson 1978). Community analysis suggests that two groups of photophytic climbers occur, namely early successional climbers and forest-dwelling or climax member lianas. Although growth and reproduction of both groups is generally greatest under high light intensities, their relative shade tolerances in the early stages of growth set them apart ecologically and determine their density and distribution in space and time. Members of the first group may be herbaceous or woody. Obligate heliophytes, they cannot tolerate deep shade at any stage of their life cycle. Leaves are retained along the entire shoot and individuals are frequently shrubby but may climb to heights of 20 m or more. These species are associated with secondary successional areas such as forest margins, large gaps, watercourses, and clearings, where they form dense stands. Many Passiflora spp. belong to this group. The second group are facultative sciophytes, generally "woody" (including some monocotyledons), have a shade tolerant juvenile stage and inhabit the interior of closed canopy climax forests. Upon reaching higher light intensities, they respond by branching profusely. Lower leaves are not retained once the canopy is reached (Richards 1952: Jones and Gray 1977).

Much of the biomass of larger lianas is found in the upper canopy layers where it may be largely imperceptible (Brender 1961; Janzen 1971; Choudhury 1972). In the mid to lower stratas (B story of Richards 1952) highly branched lianas often form a closed canopy with nearby trees through which the emergents project (Fogge 1960; Walter 1971). Richards (1952) noted that the increase in canopy coherence furnished by lianas leads to greater amounts of shade cast on the forest floor, stabilizing the microclimate. In contrast, Ogawa et al. (1965b) found that the overall standing biomass in a sample of the Asian monsoon forest was stable at carrying capacity and independent of the relative densities of climbing and arborescent species, suggesting that total cover may not increased by the presence of lianas in the forest, as suggested by Richards. Rather, lianas compete directly with trees, replacing an equivalent amount of biomass (leaf).

A significant impact of vines on forest structure is the reduction in leaf biomass of certain trees as a result of shading by liana canopies. A lessening of the ratio of support to dependent biomass lowers the photosynthetic capacity of the host tree; vigor is adversely affected and premature death of healthy trees may result. In this manner, succession may be accelerated even though the total biomass is stable (Webb 1958; Ogawa et al. 1965a,b; Penfound 1966). The host tree's photosynthetic area is also decreased when the weight of lianas breaks large tree branches, often allowing the entrance of pathogens (Wong 1971a; Lowe and Walker 1977). Vines also promote the collapse of weakened or dead trees; conversely they often tie tree crowns together, increasing canopy coherence and preventing the fall of

trees (Jones 1955,1956; Fox 1968). In a study of the effects of lianas on the growth, reproduction and species composition of trees subsequent to gap formation, Putz (1982) found that lianas greatly increased tree mortality rates and decreased diameter growth and regeneration rates of canopy trees. Species composition (trees) was also affected.

Secondary Forests

The rapid growth of climbers following disturbance to the canopy is a characteristic feature of sunny, open sites and considered, by some authors, an expression of heliophily in these species (Richards 1952; Fogge 1960; Walter 1971). Canopy disturbance resulting in higher light intensities on the forest floor stimulates the germination of seeds present in the soil as well as the release of suppressed individuals (Meijer 1970; Liew 1973a; Jones and Gray 1977). Although tropical rain forests popularly conjure visions of dense liana curtains festooning the forest, this phenomenon is largely restricted to successional areas. Openings created when a canopy or emergent tree falls and forest edges adjacent to roads, clearings, rivers and similar areas are frequently blanketed with the growth of vines.

Liana thickets represent a pioneer or seral stage in succession; evidence gathered by workers throughout tropical regions suggests that succession favors replacement of these heliophytic species (Greig-Smith 1952a,b; Dawkins 1961; Budowski 1965; Gomez-Pompa et al. 1972). The presence of liana thickets following large scale natural disturbances are a regular feature of areas where cyclones, hurricanes and fire are recurrent and natural succession is held back by frequent disturbances (Webb 1958; Jones and Gray 1977; Crow 1980). Webb (1958) noted that the presence of dense liana tangles in the Queensland rain forest of Australia was related to past cyclone damage. The regular occurrence of these "cyclone scrubs" was dependent upon intermittent defoliation of canopy trees by cyclones creating large gaps in the forest.

After studying gap size and related species composition, Poore (1968) and Denslow (1980) concluded that large gaps were colonized by early successional species while small isolated gaps were quickly filled by surrounding late sucessional species. Gap size is strongly correlated with past forest disturbance and future successional patterns. Fundamental differences exist in the environment created by large and small clearings, affecting the differential establishment probabilities of individuals. Gap size is dependent upon the rate and scale of a disturbance regime; natural disturbances in the forest interior most often lead to the formation of gaps which are small in relation to plant size. Many plants found in these forests have life histories adapted to these disturbances (Denslow 1980; Wallace and Dunn 1980). Those lianas which are a regular feature of the forest interior regenerate in a patchwork pattern, after small gap invasion, in a situation largely analagous to many tree species (Grubb 1977).

Successful gap invasion involves a complex of factors including nearness of parent tree (or vine), dispersability, phenological behavior, seed dormancy, viability and germination characteristics, relative shade tolerances and growth rates. These factors vary in space and time. New species combinations are dependent upon the species present at the time of gap formation, their stage in the life cycle and interspecific competition with invading species (Poore 1968; Liew 1973a; Horn 1974; Grubb 1977).

Several authors, studying the effects of logging on tropical forest regeneration, noted that many lianas cannot regenerate in the shade of secondary successional species and are dependent upon large-scale disturbances for population maintenance (Jones 1955,1956; Fogge 1960; Nicholson 1965). In the same Australian forests where "cyclone scrubs" are found, occasional, isolated windthrows create small gaps which are rapidly closed by the release of suppressed tree saplings. The result is a closed canopy forest with a normal vine cover (Webb 1958). These findings agree with those of MacGregor (1939, in Jones 1956).

The frequency of liana thickets has increased with the escalation of man's recent activities in tropical forests. Land clearing for logging operations and crop production is regularly followed, shortly thereafter, by climber infestation (Dawkins 1961; Nicholson 1965; Kochummen 1966; Fox 1968; Meijer 1970.) Although most reports indicate that lianas are eventually replaced after the disturbance ceases, they may exert considerable influence on the nature of post-disturbance communities (Jackson 1956; Jones 1955,1956; Jones and Gray 1977). Regrowth may be structurally similar but vary widely in species composition from the original vegetation (Ewel 1980). Long term trends could be affected by the presence of low numbers of persistent adults which remain, providing a seed bank for future invasions (Jones 1955,1956; Nicholson 1965). Increasing the frequency of disturbances favors regeneration of these remnant individuals over their eventual replacement by climax species.

Trees in all size classes suffer injury from climbers but in secondary successional situations, the heaviest damage occurs to seedlings and saplings, often resulting in a retarded rate of regeneration. Jones (1955,1956) working in Nigerian forests, noted that masses of climbers which develop, after logging, in the crowns of regenerating young trees may deform entire areas of saplings. Similar findings were reported by Fox (1968). In some Australian forests, climbers reportedly stunt, shape and strangle young trees, restricting apical growth, reducing competitive ability and, in some cases, resulting in the death of saplings (Jones and Gray 1977). Investigations by Lowe and Walker (1977) suggest that the mode of tree growth may lend a competitive advantage over lianas. Monopodial forms gain in height more rapidly, escaping climber infestation, while slower growing sympodial forms succumb to fast growing climbers. Putz (1982) reached a similar conclusion, noting that some trees were not

susceptible to liana infestation due to their growth rates, growth forms or mechanical flexibility.

Montane Rain Forests

Tropical montane rain forests differ in structure and species composition from their lowland counterparts. As elevation increases, temperature decreases and largely because of cloud immobility, humidity increases. Much of the water supplied to plants is in the form of fog or fog drip and its frequency is the most important factor in determining plant formations (Grubb and Whitmore 1966; Walter 1971). Decreased temperatures and low light intensities due to heavy fog decrease the intrinsic rate of growth resulting in a forest of lower stature and biomass yield per hectare when compared with lowland forests (Grubb and Whitmore 1966; Etherington 1975). A gradual thinning or disappearance of the upper canopy layer accompanies the overall decrease in height of the forest (Richards 1952). Consequently, these forests are usually simpler in structure with increasing elevation until the vegetation becomes basically a scrub community, as in the paramos of Latin American highlands. While species richness is lower in most montane forests, there generally is no trend towards single species dominance as in many lowland rain forests (Richards 1952). Slow rates of growth following disturbance to these areas make them more susceptible to invasion by fast-growing exotic species (Ewel 1980).

The role of climbers in montane rain forests has seldom been investigated. Richards (1952) stated that as elevation increases (in tropical areas) lianas become rarer and eventually disappear. In contrast, there is an abundance of climbers and epiphytes in the crowns of most trees in montane rain forests of Ecuador (Grubb et al. 1963). When comparing these forests with lowland ones, Grubb et al. (1963) found a higher density but lower species diversity of climbers in the montane associations. Large-scale, man-induced disturbances are significantly less in the mid-elevation forests of the tropics; lower tree stature and the difficulty of access to these areas are contributing factors. The competitive relationships between lianas and climax tree species in these areas have not been investigated to date.

Hawaiian Forests

Mueller-Dombois (1975) hypothesized that the paucity of large native, woody climbers in Hawai'i results in a nearly-empty niche (functional) in Hawaiian forests, easily exploited by introduced climbers. The broad functional concept allows for the existence of empty niches where resources remain unexploited (Elton 1935,1958). Under these conditions, a species may successfully invade an area without replacement of existing species. Oceanic islands often represent exaggerated examples of this concept. Species may be added to island biota for some time before their niches overlap and competition results (Keast 1971; MacNaughton and Wolf 1973). If, as suggested by Carlquist

(1980), numerous unoccupied niches were created by the selectiveness of dispersal to the Hawaiian Islands, many exotic species would be expected to co-exist in a native plant community without competitive exclusion or dominance of the native species present.

In fact, most investigations to date support the idea that few empty niches occur in Hawaiian montane rain forest vegetation complexes. Studies show that exotic species do not rapidly invade intact forests but must depend upon fairly large scale disturbance, natural or artificial, for establishment and population maintenance (Jacobi and Warshauer 1975; Mueller-Dombois 1975; Mueller-Dombois et al. 1977; Yoshinaga 1977; Burton 1980a; Mueller-Dombois et al. 1980.). Disturbance is often in the form of canopy openings which are readily invaded by fast-growing native and exotic heliophytes. Studies elsewhere have shown that the fate of exotics is dependent upon the stability of the community and the frequency and magnitude of the disturbance (Grubb 1977; Harper 1977; Vivrette and Mueller 1977, Ewel 1980).

Montane forests in Hawai'i are low in species diversity and simple in canopy structure, tending towards single species dominance in many forests. Two ecologically wide-ranging species, Acacia koa and Metrosideros collina, dominate the emergent layer of Hawaiian forests (Yoshinaga 1977; Mueller-Dombois et al. 1981). The physiognomy of these dominants has led to forests with rather open canopies, except where tree ferns (Cibotium spp.) form a dominant subcanopy layer. Native climbers are relatively rare in these forests. In some forests, a continuous ground cover is formed at 1 to 1.5 meters by native ferns and shrubs such as lobeloids and Cyrtandra spp. but few native herbaceous species occur in the ground layer of most forests (Mueller-Dombois 1975).

Examination of several works on the Hawaiian flora reveals few large, native woody climbers (Hillebrand 1888; Rock 1913; Bryan 1915). Among the best historical descriptions of Hawaiian forests are those of Rock (1913). Several references are made to areas in which liana tangles can be found forming a dense mat of vegetation at ground level (Phyllostegia spp., Stenogyne spp.) but few of these proliferate into the canopy. Two native climbing shrubs, Alyxia olivaeformis (maile) and Rubus hawaiiensis Gray ('akala), occasionally form dense tangles, principally restricted to the subcanopy layers (Rock 1913; personal observation). Dubautia latifolia (Gray) Keck a large, native climber restricted to the Koke'e region of Kaua'i, often forms dense thickets in the canopy of host trees (Heller 1897). The most prolific native climber, Freycinetia arborea ('ie'ie) was reported by Rock (1913), to form dense tangles in some of the lower elevation forests. Observations on the growth habit of 'ie'ie reveal that tangles occur only at low levels in the canopy or at ground level. No distinct canopy is formed by F. arborea, rather, foliage occurs at regular intervals along the host tree.

Many exotic lianas have been introduced into the Hawaiian Islands (Neal 1965), but few have become economic problems. Over thirty species and varieties of the predominantly climbing genus Passiflora have been introduced into Hawai'i (St. John 1973); approximately ten of these have become naturalized and common. Presently, only P. mollissima, and P. ligularis at slightly lower elevations, are considered a threat to upland Hawaiian forests. Observations to date suggest that P. mollissima severely affects the vigor of native tree species and may actually replace them in the course of succession (Jacobi and Warshauer 1975; Scowcroft and Nelson 1976; Burton 1980b).

Climbers as Forest Weeds

Weedy taxa are frequently pioneer or seral species which respond favorably to increased light intensities. Most studies of weedy species have concentrated on economically important taxa, principally grasses and annuals. In light of the recent evidence gathered by foresters in the tropics, lianas are becoming increasingly recognized as economic forest pests (Dawkins 1961; Nicholson 1965; Kochummen 1966; Fox 1968; Meijer 1970).

Many climbers are fast growing heliophytes capable of successfully invading large gaps in the forest. An increase in the frequency of these gaps could result in the extension of areas of secondary growth climbers. Recurrent large-scale disturbances, resulting in the depletion of the seed bank of primary forest trees could eventually lead to the permanent replacement of forests by climber-scrubs in these areas. Vegetation patterns may be further altered if, as suggested by Denslow (1980), large scale disturbances favor the establishment of exotics rather than native "weeds", many of which are adapted to small scale forest disturbances. Although a large body of information has been gathered on the effects of climbers on forest succession, little demographic work has been done on the individual climber species. The only examples of this type of study are from the temperate zone, although the tropics could a great deal of information on the population dynamics of invading climbers.

Kudzu (Pueraria spp.), an asian vine, was introduced into the United States as a fast growing cover crop for eroded areas (Bailey 1944). The same characteristics which made it a succesful cover crop allowed it to become a serious forest pest within a short time after its introduction. Mature forest trees are not seriously affected by the growth of this herbaceous climber, but the regeneration of young trees is frequently slowed or halted (Bailey 1944; Telford and Childers 1947).

Lonicera japonica Thunb., a woody climber from Japan was introduced into the United States for its fragrant blooms. Fruits were widely distributed by birds and honeysuckle quickly became a problem in the forest (Thomas 1980). Growth increases

linearly with light intensity, therefore, open areas are most susceptible to invasion. Areas in which the canopy has been disturbed are easily invaded and populations are capable of encroaching upon an intact forest from the periphery. Deep shade in the forest interior severely limits growth of individuals but populations are maintained by a few shade-tolerant individuals. When populations increase in size saplings, shrubs and trees are smothered and forest regeneration is inhibited (Brender 1961; Thomas 1979,1980). Dense growth of honeysuckle affects forest structure by reducing the number of vertical layers in the community, thereby allowing more light to reach the forest floor. A favorable habitat is created for the continued growth and establishment of L. japonica which may eventually replace native climax species (Thomas 1980).

SOME ASPECTS OF THE AUTECOLOGY OF PASSIFLORA MOLLISSIMA

PASSIFLORA MOLLISSIMA IN SOUTH AMERICA

Passiflora mollissima is a woody vine, often climbing to heights of 20 m or more. The trilobate leaves are pubescent with 8-12 sessile petiolar glands. The large, pink flowers are tubular and pendant. Habit, leaf shape and leaf size are variable. Plants have often been confused with closely-related Tacsonia species, particularly Passiflora mixta L. and P. tripartita (Juss.) Poir, with which P. mollissima hybridizes in nature. Passiflora mollissima is distinguished from all but P. tripartita by its oblong, yellow fruits with soft, leathery pericarp and orange succulent arils and from P. tripartita by its leaf shape: lateral segments diverge from mid-segments at an angle of less than 75' in P. mollissima and at 90' in P. tripartita (Escobar 1980).

Taxonomic Relationships

Taxonomic history

The large, showy flowers characteristic of many of the Passifloraceae have long attracted botanists to the study of this family. Early seventeenth century explorers saw a likeness to the elements of the crucifixion in the unique structure of the flower, and named them Flos Passionis or passion flowers (Bailey 1963). Accounts of the Passifloraceae are included in many eighteenth century botanical works but the first extensive monograph of the family, by Cavanilles, was published in 1790 and included 43 species (Cavanilles 1790). Various treatments followed this original work (Jussieu 1805; Masters 1872; Triana and Planchon 1873; Harms 1925), the most recent in 1938, by Killip, on the American species.

The Passifloraceae is a natural family of tropical distribution comprised of 12 genera and over 500 species (Killip 1938). It is closely allied to the Turneraceae and Malesherbiaceae (Masters 1871; Harms 1925). Members are typically herbaceous or woody vines with highly developed tendrils. Three prominent bracts surround the bisexual, tubular flowers which contain a one-celled superior ovary. Distinguishing family characteristics include the presence of a corona, petiolar glands, the fusion of the male and female reproductive structures into a large stalk, the androgynophore, and fleshy arillate seeds (Killip 1938).

The predominantly neotropical genus Passiflora, is the largest and most important in the family, containing nearly 400 species. It has undergone many revisions during its history. Tacsonia was first recognized as a genus distinct from Passiflora by Tournefort (1700). Later, Linnaeus f. (1781) considered all passion flowers members of a single genus, Passiflora. The generic status of Tacsonia was adopted by Jussieu (1805) and maintained by Persoon (1807) and de Candolle (1828), who recognized four sections within the genus. In his extensive monograph of the Passifloraceae, Masters (1872) recognized Tacsonia as a distinct genus with two sections, Bracteogama and Eutacsonia, and 25 species. As delimited by Masters, Tacsonia differs from Passiflora by its elongate floral tube, faucial corona and a short reflexed corona or operculum at the base of the floral tube. The geographical isolation of the group also adds to its distinctiveness.

Later workers felt the characteristics of the Tacsonia insufficiently unique to elevate it to a generic rank. In a monograph of the Columbian Passifloraceae, Triana and Planchon (1873) recognized only one genus, Passiflora, with Tacsonia a subgenus. Harms (1925) subdivided the genus Passiflora into 21 sections, including Tacsonia, with many subsections and series. In the most recent taxonomic treatment of the group by Killip (1938), many of the Harms' sections have been raised to subgenera. Tacsonia is currently considered a subgenus of Passiflora with 10 sections, 40 species and 8 varieties (Escobar 1980).

Nomenclature and Synonomy

Passiflora mollissima (HBK.) Bailey was first collected in 1767 by Humboldt at Santa Fe de Bogota (Colombia) (Paxton 1846; Killip 1938) and described as Tacsonia mollissima by Humboldt, Bonpland and Kunth, in 1817. In 1916, Bailey transferred T. mollissima HBK. to the genus Passiflora. Under the current system of classification it is included in the genus Passiflora, subgenus Tacsonia, section Bracteogama (Killip 1938; Escobar 1980).

The taxonomic problems in the group and the morphological variability of individuals have resulted in number of synonyms for P. mollissima. They include (Killip 1938):

Passiflora tomentosa Lam. Encycl. 3:40. 1789.
Tacsonia mollissima HBK. Nov. Gen. & Sp. 2:144. 1817.
Murucuju mollissima Spreng. Syst. Veg. 3:43. 1826.
Tacsonia mixta subsp. tomentosa Mast. Trans. Linn. Soc. 27:629. 1871.
Tacsonia mollissima (HBK.) var. glabrescens Mast. Mart. Fl. Bras. 13, pt. 1:541. 1872.
Passiflora tomentosa var. mollissima Tr. & Planch. Ann. Sci. Nat. V. Bot. 17:131. 1873.

Several common names arose as a consequence of the cultivation of passion flowers in South America and abroad; most of these are not restricted to a single species. In South America the more popular names for P. mollissima include: curuba (Colombia, Andes); tintin, tumbo, trompos and tacso (Peru) (Killip 1938). Common names from outside the native range include: granadilla cimarrona (Mexico), passion fruit (Europe and United States) banana passion fruit (Australia, New Zealand, Africa, Hawai'i), banana liliko'i and banana poka (Hawai'i) (Killip 1938; Menninger 1970; Young 1970; de Wilde 1975).

Reproductive Biology

Cytology

In his cytological studies of 29 species and varieties of Passiflora growing in Hawai'i, Storey (1950) determined the somatic chromosome number of all horticultural taxa studied, including P. mollissima, to be 2n=18. Based on his extensive survey of the group, Storey assumed a base number of x=3, in contrast to the x=6 proposed earlier by Darlington and Ammal (1945). The unlikelihood of all species being fertile triploids, as well as the frequent hybridizations in the group, led Storey to postulate an ancient origin of the hexaploid series.

An alternative mode of evolution (Beal 1969) suggests a succession of aneuploid reductions from the 2n=24 group to the 2n=18 type. Escobar (1980) lists n=9 as the haploid number of all Tacsonia species.

Breeding systems

Little is known about the pollinators of Passiflora mollissima; they are generally thought to be hummingbirds and large bees (Escobar 1980). Unlike many passion flowers, P. mollissima is self-compatible (Scott 1865; Brizicky 1961; Escobar 1980). Escobar (1980) obtained a 40 percent fruit set for hand pollinated flowers but only four percent of the naturally selfed flowers later developed into fruits, suggesting that selfing is uncommon in nature for this species. Problems with fruit set, commonly reported for cultivated passion fruit species, particularly P. edulis f. flavicarpa Deg., have not been reported for P. mollissima (Popenoe 1920; Pope 1935; Akamine 1956).

Hybridization

Few reproductive barriers exist within the subgenus Tacsonia. Passiflora mollissima hybridizes freely in nature with other Tacsonia throughout its range, producing fertile offspring. Hybrids in the wild have been recognized between P. mollissima and P. mixta (Killip 1938; de Wilde 1975; Escobar 1980), P. mollissima and P. pinnatistipula Cav. (de Wilde 1975; Escobar 1980), P. mollissima and P. tripartita (de Wilde 1975; Escobar 1980) and P. mollissima and P. cumbalensis (Karst.) Harms (Escobar 1980). One natural and one horticultural hybrid of P. mollissima have been described: Passiflora X rosea (Karst.) Killip (=P. pinnatistipula X P. mollissima) (Killip 1938; Martin and Nakasone 1970) and P. exoniensis Hort. (=P. antioquiensis X P. mollissima) (Martin and Nakasone 1970).

Escobar (1980) has successfully crossed P. mollissima with P. ampullacea (Mast.) Harms, P. mathewsii (Masters) Killip, P. mixta, P. pinnatistipula and P. tripartita. All crosses resulted in fruit set and hybrids were vigorous with normal development. No data are yet available for fruit production or pollen viability in the hybrids.

Distribution

Passiflora mollissima is found between 2000 and 3600 m, rarely lower or higher, in the Eastern Cordillera of the Andes of Colombia, southeastern Andean slopes of Peru and the western slopes of Bolivia and Venezuela (Killip 1938; Escobar 1980). Cultivated extensively throughout South America, many populations probably represent escapees from cultivation. Most Tacsonia species are local endemics and restricted to the moist mountain slopes of the Andes (Escobar 1980). Passiflora mixta and several cultivated species, including P. mollissima, are wider-ranging and found in the drier inter-Andean valleys as well as the wet slopes. Endemicity is common in the Tacsonia and results from discontinuities in habitat due to geographical and climatic barriers. It is not clear from Escobar's (1980) description whether or not cultivated Tacsonia have wider distributions as a result of cultivation and possibly later escape or selection for cultivars was from naturally wide-ranging species. She does note, however, that "natural" populations of P. mollissima were found only in northern Peru, where the species likely originated, suggesting that its natural distribution may be more limited.

Man has disseminated this species as an ornamental and for its edible fruit to many regions, including: Mexico, California, New Zealand, Australia, Hawai'i, New Guinea, the Kermadec Islands, India, Ceylon and East Africa (Killip 1938; Martin and Nakasone 1970; Green 1972; de Wilde 1975; Sykes 1977; Escobar 1980).

Ecological Relationships: Abiotic

References to the ecology of Passiflora mollissima in its native habitat are few. Some generalizations may be drawn from accounts of its behavior as a cultivated plant, but these must be made with reservations.

Climate

The subgenus Tacsonia, to which P. mollissima belongs, is restricted, with few exceptions, to the moist upper slopes of the Andes. The climate of the high-elevation Andes is cool with frequent fog and mist; relative humidity is high. The amount of solar radiation reaching the earth is fairly constant all year but is reduced by the frequent fog characteristic of this area. Average annual daily temperatures exhibit little variation (3-6 °C). This difference is regularly exceeded by the diurnal range. Within the latitudinal and altitudinal limits of P. mollissima, average annual temperatures range from 6 to 20 °C. Rainfall is high and seasonal in most areas with one or two annual dry periods, usually between June and August. Average annual rainfall ranges from approximately 750 mm to 3000 mm.

Passiflora mollissima grows best in cool temperatures; occasional frosts, to -2 °C, are tolerated without injury. At lower temperatures injury occurs, particularly to the apices (Paxton 1846; Jaramillo 1957; Anonymous 1962; Martin and Nakasone 1970). High temperatures may also affect growth and vigor. Martin and Nakasone (1970) report that P. mollissima cultivation has been unsuccessful at low elevations in the tropics and Escobar (1980) notes that plants appear to be intolerant of higher temperatures. Temperature may also affect fecundity. Several authors have noted that flowering and fruiting are reduced or prevented by elevated temperatures (Hooker 1845; Howell 1976; Escobar 1980; Gilbert pers. comm.).

Light

Passiflora mollissima is a heliophyte, locating in open sites such as roadsides, field borders and light gaps within the forest (Escobar pers. comm.). There are no reports on the effects of light on growth or phenology of P. mollissima.

Soils

Natural populations of P. mollissima are confined to moist sites in the Andes, although an abundance of drier sites are available (Escobar 1980). Most cultivated passion fruit, including P. mollissima, reportedly "prefer" moist, well-drained soils; survival is poor when drainage is impeded (Martin and Nakasone 1970; Herklots 1975). Cultivated crops are customarily irrigated in dry areas. In cultivation, individuals produced choice fruits in a variety of soil types (Jaramillo 1957).

Ecological Relationships: Biotic

Germination

The seeds of P. mollissima are surrounded by a hard, bony testa. Reported emergence time for fresh seeds varies from less than two weeks to 14 weeks (Jaramillo 1957; Anonymous 1962). Pretreatment of seeds with warm water or weak acid reduces the germination time by 30-50%. Schoniger (1969) reports that seeds of P. mollissima fall into two distinct categories: those which germinate in five to eight weeks and those in which germination is delayed for 12 to 20 weeks. Escobar (1980) notes that seeds germinate rapidly after an initial period of latency.

Dispersal

Dispersal agents of Passiflora mollissima in its native range are unknown, but the large, fleshy fruits characteristic of this species are suggestive of mammal or frugivorous bird transport. Janzen (1968) has observed seeds of other Passiflora species in bird droppings and Escobar (1980) notes that the fruit of Tacsonia spp. are commonly eaten on the vine suggesting avian or bat dispersal. The lack of a suitable dispersal agent in the native range may be an additional factor responsible for the high rate of local endemism observed for Tacsonia species.

Community Associations

Passiflora mollissima is confined to elevations greater than 2000 m on the moist slopes of the Andes. This elevational zone corresponds with the area known as the "ceja de la montana" (eyebrow of the forest), characterized by high humidity, cool temperatures throughout the year, constant fog and moderate light intensities. The "cejas" are composed of evergreen woody formations of lower stature than the "montana". Floristically, they represent a transition between the low elevation "montana" (tropical rain forest) and high elevation cloud forests. Ferns, orchids and bromeliads are abundant and occur as epiphytes, frequently obscuring an entire host tree. Mosses and treeferns are also common. Dominant angiosperm families include the Compositae, Ericaceae and Lobeliaceae (Macbride 1936; Goodspeed 1941; Cuatrecasas 1953; Ferreyra 1953).

Passiflora mollissima is cultivated extensively, with irrigation, in the dry, inter-andean valleys and may frequently be found associated with Alnus spp. along watercourses, presumably naturalized following cultivation (Pemberton pers. comm.). The gallery vegetation may be described as an evergreen and rainy-green bushwood or shrubwood with a higher density than the surrounding vegetation. Representative genera include: Alnus, Salix, Buddleia, Sambucus, Bauhinia, Jacaranda and Piptadenia. Passiflora mollissima may also be found at the lower limits of subparamo vegetation zone, which is characterized by thickets and low tree formations alternating with meadows (MacBride 1936; Weberbauer 1936; Cuatrecasas 1953).

Predation

In his work with Passiflora in their native range, Masters (1869) observed that flowers were frequently lacerated by hummingbirds seeking nectar at the base of the tube. Escobar (1980) notes that one quarter of all species of Tacsonia she studied showed some amount of damage to the flowers. Nectar robbing is also common in Hawai'i(Pung 1971).

A number of insects attack P. mollissima but few have been considered serious pests. Of the insects known to feed on P. mollissima, the larval stage of Dione juno Cremers (Lepidoptera; Nymphalidae) is the most damaging (Escobar 1980). Individuals of Parisama sp. (Nymphalidae) have been observed ovipositing on P. mollissima but do not appear to be serious pests. Other pests in the Lepidoptera include Dione glycera Felder and Felder (Nymphalidae), Podotricha telesiphe (Hew.) (Nymphalidae), Odonna passiflorae Clarke (Oecophoricdae) and Diaphania sp. (Pyralidae) (Gilbert 1976; Escobar 1980; Clarke 1981). Flies belonging to the genus Anastrepha infect fruit and two homopterans Selenaspidus sp. and Empoasca sp. feed on leaves and fruits (Jaramillo 1958; Valero and Viana 1970; Escobar 1980). A recently described species of Diptera, Dasiops curubae Steyskal, reportedly attacks flowers and fruits of P. mollissima and related species in Columbia (Steyskal 1980). Gilbert (1976) reported an unidentified chrysomelid beetle feeding on P. mollissima in Peru. In plantations, root-knot nematodes, (Meliodygyne sp.) may also attack P. mollissima and slugs (Milax gagetes (Draparnaud)) often eat young plants (Anonymous 1962; Escobar 1980).

Disease

Several pathogens are known to attack Passiflora mollissima; Colletotrichum gloeosporioides Penz. and C. passiflorae Stevens and Young (anthracnoses), Alternaria spp. (brown spot disease) and Oidium spp. (mildews) reportedly lower yields but do not kill their host (U.S.D.A. 1960; Anonymous 1962; Tagawa 1972; Escobar 1980). Under very moist soil conditions, seedlings are succeptible to Fusarium sp. wilt (Martin and Nakasone 1970).

Economic Uses

Approximately 50 to 60 species of Passiflora bear edible fruit (Martin and Nakasone 1970). Of these, the two most widely cultivated species are P. edulis and P. mollissima. In its native range, P. mollissima is cultivated extensively for its fruit and as an ornamental (Killip 1938; Escobar 1980). Well managed arbors may yield 35,000-40,000 kg of fruit per hectare (Anonymous 1962). Juice from the fruit is high in Vitamin C and frequently used for cocktails, sherbets, and wines (Menninger 1970; Seelkopf et al. 1962). In many South American markets the fruit of P. mollissima is preferred to the more widely cultivated P. edulis (Castenada 1956).

In many cases, it is not clear whether the importation of Passiflora mollissima to an area occurred principally for the value of its fruit or its attractive flowers and foliage. Young (1970) notes only that it was offered for sale in New Zealand in the nineteenth century, presumably as a food crop. Masters (1869) was the first to remark on the insipid nature of the fruit when grown abroad. He states; "Unless under the andean sun the flavor is more decided than it is here (England), we should regard the fruits as ornamental rather than useful on the dessert table." Similarly, the fruit of the Hawaiian P. mollissima is often considered insipid (Pung 1971). Today the commercial cultivation of this species appears to be limited to South America. No pharmaceutical products or secondary plant substances have been reported from P. mollissima to date.

PASSIFLORA MOLLISSIMA IN HAWAI'I

Passiflora mollissima is currently proliferating in mid to high elevation forests on the islands of Hawai'i and Kaua'i. A perrenial climber from the Andean highlands, it is capable of climbing 20 meters to the tops of many of the tallest trees, shading their crowns with its foliage. Infestations of this plant occur in large areas of native Metrosideros collina and Acacia koa forests, inhibiting the growth and reproduction of forest trees. In a recent address to foresters in the state of Hawai'i, Skolmen (1979) declared P. mollissima the number one problem in koa forest management.

Locally, this plant is known as banana poka. The name appears to be restricted to the Hawaiian Islands and is derived from the Hawaiian word poka'a, referring to the tendrils, meaning "that which is wound up in a ball, as rope or twine" (Pukui and Elbert 1977) and from the banana like fruit it bears (Wong 1971a).

The exact date of introduction of Passiflora mollissima to the Hawaiian islands is unknown; it was first observed near the Puuwaawaa Ranch, North Kona in 1921. Later, it was reported to have been planted at several sites along the Hamakua coast, Hualalai and the slopes of Mauna Kea (Wong 1971a). The first documentation of P. mollissima in Hawai'i is from a herbarium specimen, collected by L.H. McDaniels in 1926, from the Puuwaawaa area (BISH #61463). McDaniels described the plant as "growing in an open forest, scrambling over trees", indicating that it was naturalized in the area. The first reference to P. mollissima in Hawai'i is by Pope (1929). The introduction of this plant to the island of Kaua'i occurred at approximately the same time. Wenkam (1967) notes that: "early construction workers planted the hanging pink liliko'i around their bunk dormitories for food while digging the irrigation (Kekaha) tunnels in 1923". No specimen was collected from this area until 1947 (G. Pearsall, BISH #23153).

Accounts of the Hawaiian flora prior to 1921 do not list P. mollissima or any of its reported synonyms (Hillebrand 1888; Bryan 1915). It is probable that P. mollissima, like the closely related climber, P. edulis Sims., escaped from cultivation and became naturalized shortly after its introduction. The most recent intentional introduction occurred in 1958 when a plant was taken from Laupahoehoe to Volcano, on the island of Hawai'i (Wong 1971a).

Distribution

Passiflora mollissima is found on the islands of Hawai'i, Kaua'i and Maui. In 1971, a survey team from the Department of Land and Natural Resources Division of Forestry plotted the distribution of banana poka on the island of Hawai'i. A map (scale 1:24,000) was prepared, showing 35,000 acres overrun with this weed (Wong 1971a). Infestations, expressed as the ground area covered by banana poka, ranged from 70% to 100% to areas with a density of only one to five plants per 50 acres. The heaviest infestations occurred on 22,000 acres of the Hilo and Manowaialee Forest Reserves along the Hamakua coast. Populations on Hualalai were numerous but scattered and those in the Volcano area were small and diffuse. A later assessment, made by the same agency, noted that by 1975 the area covered had increased to 85,000 acres on the island of Hawai'i. In addition 12,000 acres of the Koke'e region of Kaua'i were infested (Daehler 1975; Landgraf 1975).

Small isolated populations have been found in the Kohala Mountains (Warshauer et al. 1983) and in Pohakuloa, on the island of Hawai'i (Higashino et al. 1977). In addition, a small isolated population consisting of one adult and approximately 250 seedlings was reported from Olinda, Maui in 1971, presumably an escape from the nearby agricultural experiment station (Wong 1971b, 1973). The State Department of Agriculture promptly eradicated the population but their files indicate that plants had reappeared in the area by 1978 (Tamura 1978b) and still appear periodically (Tamura pers. comm.).

Banana poka has successfully invaded areas of diverse climate and vegetation. On the island of Hawai'i it can be found from 300 to 2500 m elevations (Landgraf 1975; Warshauer et al. in review). Temperatures in these areas range from 10 to 25 ^{o}C (mean annual temperature); annual rainfall ranges from approximately 500 mm to 5000 mm. Colonization has occurred on dry lava flows with sparse, open Myoporum scrub communities to montane rain forests dominated by Metrosideros collina and Cibotium spp. The principal vegetation types infested with banana poka on Hawai'i include both open and closed forests of Acacia koa and Metrosideros collina, mixed native species associations, tree fern forests (Cibotium spp.) and pastures.

On Kaua'i, populations are centered in Koke'e and are found in both open and closed Acacia spp. forests from 850 to 1300 m in elevation (Daehler 1975). Rainfall in these areas varies from 750 mm to 2000 mm per year; the mean annual temperature ranges from 4 to 27 ^{o}C.

Reproductive Biology

Passiflora mollissima exhibits a high degreee of fecundity. Flowers can be found during all months of the year. Large numbers of fruits are produced each year with a peak from late spring to autumn (Pung 1971). According to Wong (1971a), a 12 cm long fruit may contain 170 to 180 arillate seeds. It is not clear whether the abundant fruit set observed in Hawai'i is due principally to spontaneous selfing of individuals or the activity of biotic pollinators. Pollen of this species is large and sticky indicating that gravitational dispersal would be difficult.

No direct observations or studies of the pollination of P. mollissima have been reported for Hawai'i. Birds are commonly assumed to pollinate flowers of P. mollissima in Hawai'i although there is little evidence to support this hypothesis to date. In South America, hummingbirds pollinate flowers when probing for nectar located at the base of the long corolla tube. Although many nectivorous birds, both native and exotic, may be found in Hawai'i, none possess a bill of sufficient length to gain access to the nectar.

The i'iwi, (Vestaria coccinia (Forster)), a native, nectar-feeding forest bird, is frequently observed robbing nectar from flowers by piercing the base of the corolla tube (Pung 1971). In this way, nectar is removed without pollinating the flowers. Two additional native species of birds, the akepa (Loxops coccineus coccineus (Gmelin)) and the amakihi (Loxops virens (Gmelin)), and the exotic white eye (Zosterops japonica japonica Temminck and Schlega) exhibit similar behavior (Pung 1971; Wong 1971a). The Hawaiian crow or alala (Corvus tropicus Gmelin) also feeds on P. mollissima nectar (Giffin 1978, 1980) as well as fruit. The mechanism of pollination is unknown in Hawai'i, therefore it is difficult to assess the significance of this loss of nectar to the reproductive success of this species. Pung (1971) reports that while a majority of flowers examined possessed peck holes, these apparently had no ill effect on the maturation of the fruit.

Insects may play a role as pollinators of Passiflora mollissima. The carpenter bee, Xylocopa varipuncta Patton, frequently pollinates P. edulis f. flavicarpa in Hawai'i (Akamine and Girolami 1959; Nishida 1963). Further studies may show it to be a pollinator of P. mollissima as well.

Dispersal

Seeds of Passiflora mollissima are well adapted for dispersal by frugivorous animals. Whereas man has been responsible for the introduction of scattered populations of P. mollissima to Hawai'i, Kaua'i and Maui, local proliferation of these introduced populations is due to exotic animals which feed on the fleshy fruits. To a lesser extent, passive dispersal by water currents also results in local proliferation along streambanks (Wong 1971a). Continued, widespread dispersal of P. mollissima in Hawai'i is due principally to the activities of a single dispersal agent, the feral pig, Sus scrofa L. Studies of feral pigs and their habits in Hawai'i have disclosed that severe banana poka infestations are correlated with areas of high pig density (Wong 1971a; Giffin 1972; Baker 1975). Seedlings often germinate from pig scats, particularly along established pig trails.

The staple food of the feral pig in the Hawaiian forest is the Hapu'u (Cibotium spp.), but this may be given up entirely for fruits such as banana poka when they are in season (Giffin 1972). Field observations by Giffin (1972) suggest that large numbers of pigs may move moderate distances to feed on fruit. Pigs may even hunt aggressively for fruit and have been observed grabbing vines and shaking them vigorously until the fruit falls, whereupon it is eaten (Giffin 1972). Although estimated home ranges in the forest are small, (one to two square miles), pig movements are often random and densities sufficient to disseminate seeds far from established trails. This often results in small isolated plant populations scattered throughout remote forest areas.

On a yearly average, P. mollissima was found to constitute 32% (by volume) of the diet of pigs censused in the Laupahoehoe area (Giffin 1972). As P. mollissima reaches its greatest population density in this area, the figure above probably represents the upper limit in the diet of the feral pig. In Hawai'i Volcanoes National Park where plant densities are considerably lower, Baker (1975) reports that only 1.5% of the diet is composed of banana poka. He does note, however, that where P. mollissima is present, its seeds are abundant in pig scats.

Many game and forest birds, both exotic and to a lesser extent native, likely disperse seeds of Passiflora mollissima and may be responsible for the establishment of isolated populations. Cattle (Bos taurus L.) and horses (Equus caballus L.) may also contribute to the spread of this species.

Association with Forest Disturbance

Vines commonly exhibit rapid growth following canopy disturbance resulting in a dense tangle of vegetation which smothers undergrowth (Jackson 1956; Nicholson 1965; Ogawa et al.

1965a,b; Kochummen 1966; Fox 1968; Meijer 1970). This situation is most prominent in tropical regions where vines are a significant component of many vegetation types (Richards 1952; Ogawa et al. 1965b). Several studies of native forest communities in Hawai'i have indicated that spread and dominance of banana poka, an opportunistic species, is aided by factors which tend to disturb the over and understory vegetation (Jacobi and Warshauer 1975; Scowcroft and Nelson 1976; Mueller-Dombois et al. 1977; Burton 1980b).

In a study of Acacia koa regeneration following logging in the Laupahoehoe Forest, Scowcroft and Nelson (1976) concluded that although seed germination, seedling density and seedling establishment of koa were greatly enhanced by canopy and ground disturbance associated with logging, saplings were unable to outcompete individuals of Passiflora mollissima. Banana poka occurred in 80% percent of the study plots and much of the regeneration was completely smothered by vines within four years.

In a report on the 'ohi'a dieback phenomenon in Hawai'i, Mueller-Dombois et al. (1980) concluded that P. mollissima (cited as P. mixta) was a potentially damaging exotic which could "significantly interfere with the reproductive cycle of native forest plants if allowed to become abundant." 'Ohi'a dieback results in the synchronous death of large numbers of individuals greatly reducing canopy cover and encouraging the growth of heliophytic species, such as banana poka.

Jacobi and Warshauer (1975) noted a rapid increase in abundance of banana poka in the 'Ola'a Tract (Hawaii Volcanoes National Park). They emphasized that P. mollissima could pave the way for the invasion of other light-loving exotics in an otherwise closed forest. Shallow rooted emergents such as Metrosideros collina and Cheirodendron trigynum easily topple under the weight of mature vines, leaving gaps in the canopy. The additional light available encourages the growth of heliophytes, both native and exotic, in the understory.

Burton (1980b) studied the effects of experimental canopy removal on exotic species invasion in the 'Ola'a Tract. His results indicate that exotic weed invasion was proportional to increased levels of irradiance reaching the forest floor. Biomass and cover of weeds present at the onset of the study increased following canopy removal. Many species, particularly annuals, showed a decline in biomass over one year but P. mollissima exhibited a steady increase in cover with time to an estimated value of one percent of the total cover within one year.

Ground disturbance by feral pigs may give a competitive advantage to seedlings and adults of P. mollissima. Previous studies of native and exotic species interactions following pig rooting indicate that under conditions of ecological stress which accompany rooting, exotic species are often better competitors

(Lamoureux and Stemmerman 1976; Warshauer 1976; Smith and Diong 1977). In a study of a subalpine grassland on Maui (Jacobi 1981), native species competed equally in pig disturbed areas, but with continued disturbance over time, the absolute cover of several exotic species in the area increased while the cover of native species decreased. These results concur with Spatz and Mueller-Dombois (1975).

Pig rooting may result in severe disturbance to existing soil and vegetation. Exotics, commonly pioneer species in their native habitats, are often better able to colonize these disturbed areas. In some cases they may persist with time, excluding or seriously reducing native species' populations. Becking (1970, in Smith and Diong 1977) reports that regeneration of the dominant native tree species, Acacia koa and Metrosideros collina is extremely slow in areas of pig disturbance and several authors have noted that pig rooting may limit regeneration of both species to epiphytic individuals (Cooray 1974; Jacobi and Warshauer 1975; Burton and Mueller-Dombois 1982). The detrimental effect of this competition on long term forest succession is an important problem in Hawaiian forest ecology today.

History of Control Measures in Hawai'i

Several small scale projects aimed at control of banana poka in Hawai'i were initiated by the Department of Land and Natural Resources, Division of Forestry, in the early 1970's. The results of many of these projects were inconclusive. The first effort by foresters involved a test of various herbicides including 2,4-D, Tordon 212 and Paraquat. Although all proved effective against P. mollissima the lack of selectivity of these herbicides represented a danger to native plants growing in the area and the project was abandoned as unfeasible (Landgraf 1971; Cusset 1975).

After rejecting chemical control methods, foresters began to look for potentailly damaging biological agents occurring in Hawai'i. Several species of Alternaria, an imperfect fungus, were discovered attacking the flowers and fruits of individuals of P. mollissima in the Hualalai area (Laemmlen 1971). The fungi were reported as quite harmful to P. mollissima but the extent of damage by these organisms was never assessed. Alternaria spp. are also reported as pathogens on P. mollissima in other areas of its range, where they have been a limiting factor in fruit production (Anonymous 1962; Jaramillo 1957). In 1973, a scale insect (Ceroplastes cerripidiformis Comstock; barnacle scale) was found on P. mollissima. Attempts at cultivation of this scale for biological control were unsuccessful and later discontinued. To date, no follow-up work has been done on these organisms.

Later, Agraulis vanillae L., a member of the Heliconiidae (passion vine butterfly; Lepidoptera) and an accidental introduction to Hawai'i, showed promise as a control agent.

After its introduction, population growth was explosive and individuals were commonly observed at low elevations on Passiflora suberosa and P. foetida. Controlled studies on the feeding habits of this species in Hawai'i showed that A. vanillae would feed on several species of Passiflora, including P. mollissima (Murai 1977; Nakahara 1977).

An attempt to introduce this organism into Koke'e, Kaua'i to control banana poka has not been successful. Agraulis vanillae is well established and abundant on P. manicata (Juss.) Pers., a sterile cultivar growing in the Koke'e area, but no butterflies were found ovipositing on P. mollissima nor were larvae observed feeding on any part of the plant (Bianchi 1979). The lack of predation by Agraulis vanillae on individuals of P. mollissima in the wild, coupled with the introduction to Hawai'i, in the earlier part of this century, of numerous parasites on Lepidoptera larvae, suggests that this species may not be a successful bio-control agent. Whereas the association of this group of the Lepidoptera with members of the genus Passiflora is well documented for Central and South America, where both plant and insect are native (Gilbert 1975; Benson et al. 1976; Benson 1978), their effectiveness as biological control agents under Hawaiian conditions is uncertain but warrants further study (Waage et al. 1981).

The first serious attempt at biological control research appeared in the form of a legislative proposal to appropriate money to search for an agent in the native range of P. mollissima. This measure did not pass the 1980 legislature but subsequently passed in 1981. In the same year, the Hawaii Dept. of Land and Natural Resources, Div. of Forestry, the Institute of Pacific Island Forestry and the National Park Service have initiated a joint research project to study the potential for biological control of P. mollissima in Hawai'i.

SUMMARY AND CONCLUSIONS

Many tropical lianas are fast-growing heliophytes; following a disturbance to the canopy, a drastic increase in liana biomass and leaf area is frequently observed. Although lianas are important components of undisturbed, primary forests, evidence gathered to date suggests that the persistence of dense liana tangles is largely restricted to open areas with a history of repeated disturbances (Webb 1958; Dawkins 1961; Budowski 1965; Crow 1980).

Hawaiian montane forests are structurally simple and lower in species diversity than many tropical forests. Frequently, canopies are rather open and light levels at the floor of many forests exceed those found in other tropical forests (Burton and Mueller-Dombois 1982). Disturbance by man and feral animals has become commonplace in Hawaiian forests and exotic species frequently compete with natives for dominance in these areas.

Passiflora mollissima, a woody climber from the Andes, has successfully invaded both disturbed and undisturbed forests in Hawai'i and is continually extending its range primarily with the aid of exotic dispersal agents. The need for control of this aggressive species has been recognized by federal and state agencies.

CHAPTER TWO

MORPHOLOGICAL VARIATION IN THE INTRODUCED VINE, PASSIFLORA MOLLISSIMA (HBK.) BAILEY IN HAWAI'I

INTRODUCTION

The liana Passiflora mollissima (HBK.) Bailey is extensively cultivated in the South American Andes and has been introduced to many subtropical and tropical mountainous areas. Considerable morphological variation exists over the wide latitudinal and altitudinal range of this species.

Reproductive barriers between species of Passiflora subgenus Tacsonia are weakly developed and P. mollissima hybridizes naturally with the closely-related taxa, P. cumbalensis (Karst.) Harms, P. mixta L.f., P. pinnatistipula Cav. and P. tripartita (Juss.) Poir, in various parts of its range, producing fertile offspring (Killip 1938; Escobar 1980). Cultivars and wild populations which are morphologically and/or ecologically distinct have been noted but no sub-specific taxa have been formally described (Seelkopf et al. 1962; Escobar 1980; Pemberton pers. comm.). One taxon, originally described as a species, was later reevaluated and designated a hybrid, P. X rosea (Karst.) Killip (Killip 1938).

Escobar (1980) noted that the morphological variability of P. mollissima and frequent hybridization, often followed by introgression, has produced individuals which are "difficult to key". Similar problems with the identification of P. mollissima and related species are found in areas where they have been introduced and have subsequently become naturalized. East African material identified as P. mollissima comprises two easily segregated forms: typical P. mollissima and an undescribed form which is possibly a hybrid with some related species (de Wilde 1975). Similarly in New Zealand, two distinct forms, one naturalized and another widely cultivated for its flowers and fruit, are known by the name P. mollissima (Young 1970).

Green's (1972) key to the native and naturalized species of Passiflora in Australia and the Pacific does not include P. mollissima, however, specimens of P. mixta, a variable species, closely resemble the Hawaiian material of P. mollissima. A similar "type" is found in New Guinea.

The Hawaiian material has been called P. mollissima or P. mixta. Fosberg (1975) noted that the taxon found in Hawai'i was not an exact match with either P. mollissima or P. mixta but was "closest to Tacsonia quitensis Benth." (synonomous with P. mixta). The name P. mixta was subsequently used in some early publications (Mueller-Dombois 1975; Mueller-Dombois et al. 1980). Specimens from Hawai'i were identified as P. mollissima by Tillet (1976) who suggested they may well represent a hybrid or introgressed form.

The atypical morphology of the Hawaiian representatives of P. mollissima has led to uncertainty and disagreement about the identity and nature of the taxon found in Hawai'i. Control of this exotic, weedy liana in Hawaiian forests will be dependent upon a successful biological control program which, in turn, is dependent upon the introduction of a highly host-specific predator or pathogen (Bosch & Messenger 1973). Determination of the correct taxonomic status of the variously named Hawaiian taxon is a critical initial step in any biological control work.

MATERIALS AND METHODS

The following morphological characters were measured on fresh specimens of a random sample of one hundred individuals of P. mollissima: maximum length and width of stipules, leaf blades, sepals, petals, fruit and seeds; maximum length and diameter of hypanthium, maximum length of trichomes, petioles, peduncles, bracts and subterminal arista (of sepals); number of stamens, stigmas, glands per petiole and seeds per fruit. In addition, fresh and dried plants from Hawai'i were examined and the general form and variability in qualitative characters such as extent and type of vesture, floral morphology and the attachment of petiolar glands were noted. These data obtained were used to prepare a description of the Hawaiian population.

This description was compared with a photograph (NY!) of the isotype of P. mollissima (P; holotype at Berlin destroyed-Escobar 1980) and 64 specimens of South American origin obtained from the herbaria of the Smithsonian Institution, Chicago Field Museum and the New York Botanical Gardens. The Hawaiian material was also compared to the original species description, by Humboldt, Bonpland and Kunth (1817), of this taxon and more recent descriptions by Killip (1938) and Escobar (1980). An additional 220 specimens of those species which hybridize with P. mollissima, including P. mixta, P. cumbalensis, P. pinnatistipula, and P. tripartita, were also examined.

Specimens from New Zealand (cited by Young 1970) and East Africa were obtained from the Herbarium of the Auckland Institute and Museum and the East African Herbarium, respectively, and compared with Hawaiian material.

Specimens of Passiflora mollissima, collected on Hawai'i and Kaua'i, were sent to Dr. L. K. Escobar, in Colombia, for identification.

RESULTS

The Hawaiian Passiflora mollissima is a morphologically variable taxon but most quantitative characters which were measured fall within the range of South American populations of this taxon (Table 1). Although Hawaiian material is similar to P. mixta, with which it has been confused, it is closest to P. mollissima (Table 1). Major quantitative difference between

the Hawaiian populations and those of South America, include a shorter calyx tube, longer sepals and fewer petiolar glands (Table 1) in the Hawaiian representatives. Qualitative differences include the general lack of pubescence on upper leaf surfaces and caducous stipules in Hawai'i. A complete description of the Hawaiian representatives follows.

Passiflora mollissima (HBK.) Bailey

Liana or woody vine, climbing to 20 meters. Entire plants sparsely to densely villous except for the upper leaf surfaces which are glabrous, glabrate or sparsely villous and flowers which are glabrous; vesture composed of straight to wavy, transparent, colorless to golden trichomes, mostly 0.4-0.6 mm long. Stems terete, striate. Stipules caducous, foliar, subreniform, 0.5-2.0 mm wide and 4.0-7.0 mm long, acuminate, aristate, glandular-dentate. Leaf blades cordate at base, (5.1-) 12.1 (-18.7) cm long, (8.1-) 17.8 (-29.5) cm wide, three-lobed from one-half to greater than three-fourths their length, lobes lanceolate to ovate, spreading, apices and sinuses acute, glandular-denticulate at margins, coriaceous, major veins impressed on upper surface and prominent on lower surface, lower surface usually densely villous, upper surface usually glabrate. Petioles canaliculate, (1.2-) 3.3 (-6.7) cm long, bearing on their posterior surface 4-9 obscure, sessile to subsessile glands, occasionally wanting. Peduncles slender, villous, (1.5-) 3.6 (-6.6) cm long. Bracts ovate, (3.3-) 4.2 (-4.9) cm long, united one-fourth to one-half their length, margins entire.

Flowers solitary in leaf axils, pendant, glabrous; calyx tube cylindrical, (0.8-) 1.0 (-1.2) cm in diameter, (4.7-) 7.0 (-8.0) cm long, dilated at base, olive green and occasionally red-tinged without, white within; sepals 5, obovate, (3.8-) 5.2 (-5.9) cm long, (1.4-) 1.9 (-2.5) cm wide, apices tapering with a subterminal arista 2mm long, pale pink to magenta; petals 5, subequal to sepals and similar but lacking aristae; perianth reflexed during anthesis; corona in one series, a purple band with white tubercles or crenulations, operculum white, dependent: stamens 5, versatile; ovary oblong, downy; placentation parietal; stigmas 3, discoid.

Fruit elliptic to ovate, (7.3-) 9.9 (-13.2) cm long, (2.4-) 3.4 (-4.1) cm wide, yellow at maturity with soft, downy, leathery pericarp, less frequently green at maturity with a tough, glabrous leathery pericarp. Seeds arilate, broadly obovate, (5-) 6 (-7) mm long, 4 (-5) mm wide, laterally compressed, reticulately pitted on both sides, dark brown at maturity, (44-) 140 (-200) per fruit; arils fleshy, translucent, orange.

DISCUSSION

The above description of the Hawaiian population of Passiflora mollissima generally agrees with Degener et al.

(1973). Values presented here usually approximate Degener et al.'s mean, except for the number of petiolar glands, which was found to be fewer and more variable in this study. In addition, the current study denotes the variability in several quantitative characters.

A comparison of the morphology of the Hawaiian material and South American populations of P. mollissima reveals that most characters of the former fall within the range of characters of P. mollissima, as most recently delimited by Escobar (1980). Escobar's work is supported by extensive field observations in South America. The quantitative characters of Hawaiian and South American populations illustrate the inherent morphological variability in this taxon (Table 1). Certain characters (leaf length and width, peduncle and fruit length and perianth size) exhibit a wide range of values in both geographic areas. Generally, characters are more constant within the Hawaiian material, with the exception of several (leaf width, petiole and fruit length) which are more variable and on the average, slightly larger in Hawai'i. The slightly larger size of leaves, sepals and petals in the Hawaiian population may be an artifact of sampling techniques: only fresh specimens were measured in Hawai'i, however, well-prepared herbarium material undergoes minimal shrinkage.

The nature of the fused calyx tube, or hypanthium, particularly the ratio of its length to that of the free sepals (and petals), is often a diagnostic character in the subgenus Tacsonia (Escobar 1980). This ratio differs in typical Hawaiian and South American specimens: in Hawai'i, the ratio is invariably below 1.5:1 while in South America it ranges from 2:1 to 3:1 (Killip 1938; Escobar 1980). This difference results in a divergence in the general appearance of flowers from the two areas (Figs. 1-2). Flowers with relatively short calyx tubes, dilated at the base and long (free) sepals which are reflexed at anthesis (Fig. 1) are characteristic of the Hawaiian population and the most common form observed in Peru and Ecuador (Escobar 1980; Pemberton pers. comm.). Although quite variable throughout the native range, typical South American floral morphology is not known from Hawai'i. The atypical flowers of the Hawaiian population have undoubtedly been responsible for much of the confusion surrounding the identity of this taxon.

While leaf size and shape are variable in Hawai'i and South America, leaves are generally more deeply-lobed and lobes more lanceolate (vs. ovate--Figs. 1-2) in the Hawaiian population. In South America, leaves are typically densely pubescent on both surfaces, but glabrous upper leaf surfaces occasionally occur (Killip 1938; Escobar 1980). Upper leaf surfaces are invariably glabrous or glabrescent in Hawai'i. This latter character probably misled workers to identify the Hawaiian taxon as Passiflora mixta, which is similar in morphology to P. mollissima but generally has glabrous upper leaf surfaces.

Several additional discrepancies deserve note. The large, prominent stipules characteristic (and diagnostic) of Passiflora mollissima are similar in form in both populations but are generally persistent in South America and invariably caducous in Hawai'i. Petiolar glands are fewer in number, more obscure and more dimunitive in the Hawaiian population; occasionally they are absent. Finally, individuals from South America are generally densely pubescent on all surfaces (except flowers). In contrast, the pubescence is often missing or sparse on Hawaiian plants.

When South American material was examined for the presence and frequency of the atypical characters described above, one specimen out of 64 was considered a good match with the Hawaiian material (Stork & Horton 9949, F!; from Peru). The frequency of single atypical characters was higher. For example, twenty percent of the specimens had glabrous upper leaf surfaces, ten percent had lanceolate leaf lobes, three percent had caducous stipules.

The general similarity between the Hawaiian representatives and P. mollissima as delimited by Escobar (1980) and the existence of a South American specimen which matches the Hawaiian type have led me to conclude that the taxon in Hawai'i is P. mollissima sensu lato and likely originated from the southern portion of the range (Peru). The lack of variability of certain characters which distinguish the Hawaiian form probably represents a highly inbred line from a very small number of initial propagules. Support for this hypothesis comes from Escobar (pers. comm.), who noted that Hawaiian specimens (LaRosa 104, 112-BISH) were atypical but representative of the area around Paucartambo Peru. Other evidence (Chapter 3) indicates that the invariability of the Hawaiian material is not due to apomictic fruit set. As earlier described by Killip (1938) and Humboldt, Bonpland and Kunth (1817), P. mollissima represented a more narrowly circumscribed taxon than that described by Escobar (1980).

Although less likely, that morphological differences in the Hawaiian representatives could have arisen through hybridization, as suggested by Tillet (1976), cannot be ruled out by this study. Passiflora tripartita shares the following morphological characters with the Hawaiian taxon, suggesting that it could be the putative parent: glabrous upper leaf surfaces, early caducous stipules, linear-oblong leaf lobes, swollen base of the calyx tube, petioles lacking glands (on rare occasions) and orange succulent arils.

Brief mention should be made of the similarity between the Hawaiian representatives of P. mollissima and several forms of Passiflora introduced to other Pacific areas. Although Green (1972) considered all Pacific taxa (including Hawaiian) in this complex as forms of the variable P. mixta, the Hawaiian form is closest to P. mollissima. As there has been considerable

confusion between P. mollissima and P. mixta, the taxa are here distinguished. Passiflora mixta may be distinguished from P. mollissima by its longer, pubescent calyx tube, stout peduncles which bear erect or horizontal flowers, slightly longer coronal filaments, fruit which are green at maturity and have a tough, leathery pericarp and scant yellowish or pale orange arils and its much smaller seeds (Table 1) (Tillet 1976; Escobar 1980; Pemberton pers. comm).

Many of the unidentified forms from New Zealand and East Africa are similar to Hawaiian material and probably represent forms of P. mollissima rather than P. mixta. Specimens from New Zealand included three distinct forms: typical P. mixta, typical P. mollissima and a form known by nurserymen in the area as yellow banana passion fruit or P. mollissima, which is a good match with the Hawaiian material. East African material (Kenya) was representative of typical P. mollissima, a form similar to the "Hawaiian type" and an intermediate form. Although material from New Guinea was not available, it is reportedly similar to that found in Hawai'i (Green 1972).

In conclusion, the Hawaiian material is herein considered Passiflora mollissima sensu lato.

CHAPTER THREE

THE BIOLOGY AND ECOLOGY OF *PASSIFLORA MOLLISSIMA* IN HAWAI'I

INTRODUCTION

Passiflora mollissima is a woody climber from the Andean highlands (2000-3600 m), extensively cultivated for its fruit and commonly found as an escape; indigenous populations are infrequent and limited in size (Escobar, pers. comm.).

Since its introduction to Hawai'i early in this century, *P. mollissima* has spread rapidly and now occupies more than 500 sq km (Warshauer et al. 1983). Infestations range from scattered individuals with low cover (10%) to complete dominance in some areas (100% cover). Few populations show any signs of decreasing.

Little is known about the life history of this important forest pest. This study investigates various stages of the life cycle and life processes which affect the adaptation and survival of each stage. The information is then used to predict which factors act to limit or foster the spread of *P. mollissima*.

General Site Descriptions

Field research was conducted in three areas on the island of Hawai'i (Fig. 3). All sites are located between 1100 and 1850 m elevations in moist, (1000 mm annual precipitation) tropical montane environments characterized by cool temperatures, frequent fog and high relative humidity. The three areas, Kaloko, Laupahoehoe and 'Ola'a, represent major centers of infestation of *Passiflora mollissima* on Hawai'i. Sites differ principally in the quantity of the annual rainfall (and seasonal distribution), the degree of canopy closure, amount of disturbance and the degree of infestation. Site selection was also dependent upon ready access and the presence of sizable populations of *P. mollissima* with all age classes represented. The general features of each site are described below.

Kaloko

Kaloko is located on the leeward slope of Mt. Hualalai from 1100 to 1500 m elevation. Site access is via Kaloko road, located 1.5 km north of Palani Junction off Mamalahoa Highway. Topographic relief in the area is generally less than 15 percent.

The mean annual temperature averages 14.9 ^{o}C. Rainfall averages 1000 mm per year (Fig. 4) and is chiefly a result of convectional rains. Winter kona storms contribute most of the rainfall received during the short wet season (March-June) (Blumenstock 1967).

Soils in the area are classified as oxisols or inceptisols. An extremely thin, acidic (pH 4.5-5.0) stony muck (Lalaau series; Sato et al. 1973) underlain by recent 'a'a lava covers approximately 50% of the study area. Other portions are covered by soils of the Puukala and Kiloa series (Sato et al. 1973). The former is a shallow, slightly acidic (pH 5.1-6.0) silt loam underlain by ash or pahoehoe lava; the latter is a stony muck (pH 6.6-8.4) underlain by 'a'a lava and occurs at elevations below 1200 m. All soils are highly permeable (Sato et al. 1973).

The vegetation is composed of a closed, tall-statured Metrosideros collina (J. R. & G. Forst.) Gray forest with a subcanopy of native trees, including Ilex anomala H. & A., Coprosma spp. and Myrsine lessertiana A. DC. and an understory of Cibotium spp., Gouldia terminalis (H. & A.) Hbd., Psychotria hawaiiensis (Gray) Fosb., Styphelia tameiameiae (Cham.) F. Muell. and Vaccinium spp. At upper elevations, scattered remnants of Acacia koa Gray forests are interspersed with Metrosideros. Exotic grasses, including Microlaena stipoides (Labill.) R. Br. and Holcus lanatus L., form the dominant ground cover except where fragmentary 'a'a lava is overlain by very thin soil. In these areas, a dense cover of bryophytes predominates. The recent Kaupulehu lava flow (1801) intersects the study area, extending from the northeast to the southeast corner. Soils in this area are very shallow and rocky (Lalaau series) and the vegetation, although very similar in composition, is simpler in structure and lower in stature than the surrounding forest.

There is little disturbance in the area. Several small sites (generally one acre) were cleared for pasture and are still relatively open compared with surrounding areas. Impact from road construction in the 1970's was minimal and exotic species invasion is restricted to a narrow corridor on either side of the road. Few exotic species, with the exception of P. mollissima and several grasses, have invaded the forest interior. Damage from feral pigs is sporadic and largely absent from areas covered by rough 'a'a lava.

Laupahoehoe

The Laupahoehoe study area lies in a seasonal forest within the Hilo Forest Reserve on the exposed, northeast flank of Mauna Kea, between 1250 and 1850 m elevation. Access is via a logging road (Blair) which begins at the lower forest reserve boundary, at Laupahoehoe, and proceeds upward. Topography consists of alternating slopes and ridges with gradients of 10 to 30 percent.

Annual rainfall averages 2151 mm with a dry season from May to July and a shorter dry period in September (Fig. 4). Frequent afternoon fog probably contributes significantly to the annual precipitation. Average annual temperature in the area is 12.7°C.

Soils are oxisols formed from volcanic ash and characteristically are deep (1-1.7 m) and well-drained (Sato et al. 1973). At elevations of 1600 m and above, soils are principally Hanipoe series silt loams. Soil pH ranges from 6.1-7.3. Below this elevation, most of the soils in the study area are acidic (pH 4.5-5.5), silty clay loams of the Puu 00 or Piihonua series. At lower elevations (< 1400 m) soils are either Maile silt loams or Honokaa silty clay loams (Sato et al. 1973). These soils are slightly acidic (pH 5.5-6.5).

The vegetation of the area is open-canopy or closed-canopy Acacia-Metrosideros forests with a subcanopy of native trees, including Cheirodendron trigynum (Gaud.) Heller, Coprosma spp. and Ilex anomala. Principal understory species include Cibotium spp., Rubus hawaiiensis Gray and Vaccinium calycinum Sw. The exotic grasses Microlaena stipoides and Holcus lanatus form a dominant ground cover in much of the lower elevation forest, while at higher elevations, the shrub and ground layers are composed of several native and exotic shrub and herb species, including Phytolacca sandwicensis Endl., Rumex giganteus Ait., Physalis peruviana L., Polygonum glabrum Willd., Rubus rosaefolius Sm. and Solanum nigrum L.

All sections of the Laupahoehoe area are heavily disturbed and P. mollissima is present in the greatest density and cover at this site. In the upper portions of the forest reserve, it forms more than 75 percent of the total plant cover (understory and overstory). Feral animals have been a major disturbance factor in the Laupahoehoe area. Much of this upper portion was heavily grazed by feral cattle prior to the introduction of P. mollissima, in 1928. Cattle were not removed from the area until the early 1940's (Bryan 1947) and domestic cattle from nearby ranches are still occasionally found in the forest reserve. Feral pigs are present in the area in high densities (Giffin 1972) and are responsible for most of the animal damage at present. In recent years, man has contributed to the disturbance. In the 1970's an area of approximately 1000 acres was logged for koa and 'ohi'a with extensive local disturbance to the overstory and understory (Scowcroft & Nelson 1976).

'Ola'a

'Ola'a is an area with little relief (5 percent) located in a tropical rain forest on the windward slope of Mauna Loa. The study area ranges in elevation from 1190 to 1250 m and is located within the 'Ola'a Tract section of Hawai'i Volcanoes National Park.

Average annual temperature at 'Ola'a is 13.9 ^{o}C. Annual rainfall averages 2880 mm with all months receiving in excess of 100 mm of rain (Fig. 4). Precipitation is largely the result of orographic rainfall and is frequently supplemented by fog and dew. A drier season occurs between June and October during which

precipitation is chiefly the result of occasional tropical storms (Blumenstock 1967).

Soils in the area are all ash-derived inceptisols of recent volcanic origin (Sato et al. 1973). Most of the study area (65%) is covered by a deep (1-1.3 m) silt loam of the Puaulu series. Approximately 10% of the study area is covered by silty clay loams of the Akaka series. Both of these soils are composed of alternating layers of ash, cinder and pumice. Another soil type, the Kahaluu series shallow (0.6 m), organic ash soils underlain by pahoehoe lava, are also common in the area. All soils are moderately well-drained and acidic (pH 4.5-6.5) (Sato et al. 1973).

Three vegetation types, differing principally in their relative cover of Metrosideros and Cibotium, are represented in the study area: scattered, open and closed Metrosideros forests. Species composition is similar in all three. The ground cover consists of scattered ferns, including Asplenium spp., Athyrium microphyllum (Sm.) Alston, Diplazium sandwichianum (Pr.) Diels, and Dryopteris spp., and Peperomia spp. Dominant shrubs include Broussaisia arguta Gaud., Cyrtandra spp., Rubus hawaiiensis and Vaccinium calycinum. The subcanopy is formed by Cibotium spp. and various native trees, including Cheirodendron trigynum, Coprosma spp., Ilex anomala, Perrottetia sandwicensis Gray and Pipturus hawaiiensis Levl. Cibotium cover is greatest in the scattered Metrosideros forest and lowest in the closed Metrosideros forest. The cover of Metrosideros is inversely proportional to that of Cibotium.

Disturbances are principally from feral pigs, which considerably damage the understory, windthrows which open up small portions of the canopy in scattered areas and 'ohi'a dieback, which affects large sections of the canopy in selected areas. Exotic species are scattered throughout the area but concentrated in disturbed areas. Most exotics are heliophytic annuals or shrubs which are greatly reduced after disturbance ceases (Burton 1980) but P. mollissima and Rubus ellipticus Sm. persist after canopy closure.

Site Selection for Population Structure and Density Estimates

Seven sites with intermediate densities of Passiflora mollissima and all age classes present were selected to study the population structure of this vine. All sites are located within the three major study areas. Sites of very low density were avoided as sampling would have been too labor-intensive. Likewise, those areas having very high vine densities (and cover) were not selected, as individual vines were impossible to differentiate and reproductive classes were very limited. The general physical features of the seven structural analysis sites are summarized in Table 2.

The principal interest at all sites is the relationship between disturbance (or lack of it) and population structure of P. mollissima. The two Kaloko sites are located near Kaloko road and support similar vegetation types, although the forest at site K1 has a greater percentage of 'ohi'a. The sites differ in the type of underlying substrate and resultant soil type. This in turn, affects the degree of feral pig activity. Site K1 is located 15 m southeast of Kaloko Rd. at 1310 m (19° 42' 36" N. Lat./ 155° 55' 47" W. Long.) in an area underlain by fragmentary 'a'a lava of fairly recent origin and a shallow soil (Lalaau series; Sato et al. 1973). The ground surface is very rocky and irregular with numerous small earth cracks. Little pig activity occurs at this site. At site K2, located 50 m west of Keanaaina Rd. at 1443 m elevation (19° 43' 05" N. Lat./155° 56' 05" W. Long.) the pahoehoe lava is much older and overlain by a deep soil (Puukala series). Pig disturbance is much greater. In addition, this site was cleared, some time ago, resulting in a more open canopy and a dominant ground cover of exotic grasses.

Site selection at Laupahoehoe was more complex. Much of the area supports a very dense population of P. mollissima, with cover in excess of 80%. Site L1 is located within the core of the infested area near the Douglas Monument, 15 m east of the forest reserve fenceline (19° 53' 48" N. Lat./155° 20' 25" W. Long.). The study area supports a much lower vine density and cover. This area appears to be a remnant of the original forest, much of which was heavily grazed and is now smothered with P. mollissima. Dominant tree species include Acacia koa, Myrsine lessertiana, Cheirodendron trigynum and Coprosma sp. The canopy is closed and canopy species are reproducing.

Sites L2 and L3 lie toward the periphery of the central infestation. Site L2 is located at the lower elevation range of the infestation, 1259 m, 45 m east of the Blair logging road (19° 55' 05" N. Lat./155° 18' 35" W. Long.). Scattered gaps occur in the Acacia - Metrosideros canopy and the site is heavily disturbed by feral pigs. This area appears susceptible to exotic species invasion due to the proximity of the access road, presence of canopy gaps and high level of feral pig activity. Site L3 is located at 1580 m elevation, approximately 5 m east of the Malua Trail (19° 51' 10" N. Lat./155° 18' 41" W. Long.). It is relatively free of human impact and has an intact canopy. Feral pig activity was present at this site but it is slightly less disturbed than site L2. The ground cover at this site is predominantly composed of the exotic grass, Microlaena stipoides.

Finally, in the 'Ola'a Tract, P. mollissima only occurred in sufficient denstities in disturbed areas. Site 01 is an area of extensive 'ohi'a dieback located at station # 38 of the U. S. Fish and Wildlife Service Transect # 31 (19° 29' 30" N. Lat./ 155° 15' 22" W. Long.). A large number of trees have died, leaving the canopy quite open. Many exotic heliophytes are found in the ground and in the shrub layers. Canopy disturbance at site 02 is restricted to relatively small gaps in the otherwise

closed-canopy treefern forest. The study area is located 0.9 km east east-northeast of the bend in Wright Rd. in the 'Ola'a Tract section of Hawai'i Volcanoes National Park (19° 28' 24" N. Lat./155° 14' 22" W. Long.). Both sites exhibit a moderate amount of feral pig activity.

METHODS AND MATERIALS

Germination

All seeds were collected from the Hilo Forest Reserve above Laupahoehoe, Hawai'i, separated from the aril and used immediately (fresh) or air dried and stored at room temperature (20-23° C) and ambient relative humidity (50-60%) for later use. Seeds were selected from the stock at random for each experiment, planted in flats or pots in vermiculite or a 50:50 mixture of soil and vermiculite and watered daily. Experiments were performed in Pope Lab greenhouses at the University of Hawai'i, Manoa and at Volcano, Hawai'i. Three replicates of each treatment were used unless specified otherwise. Germination success was based on emergence of the hypocotyl above the soil surface. Germination rate was defined as the reciprocal of the number of days to 50% maximum germination.

The effect of the aril on germination rate was determined by planting 50 fresh seeds, with and without arils, in pots and placing them under one layer of shade cloth, to prevent soil desiccation. The experiment was replicated three times.

The effect of light on germination rate and success was tested by subjecting seeds to varying intensities of natural light under ambient diurnal temperature regimes at Volcano from March to May 1980, using dried seeds collected in February 1980. Seeds were planted in flats which were placed under varying layers of nylon shade cloth in the greenhouse at Hawai'i Volcanoes National Park. A total of 30 seeds per replicate were used for each treatment. Noon light intensities ranged from 260 to 2000 uE/m2.s1. All other light intensities are expressed as percentages relative to the maximum unobstructed value: 33%, 10% and 4%. Greenhouse temperatures ranged from 43° C to 11° C, regularly exceeding natural temperatures for the area. Germination was monitored for 8 weeks.

The second experiment was conducted at Volcano from July to October 1982. Seeds for this experiment were collected in June of the same year and treated as above with the following exceptions. Each replicate consisted of 25 seeds. Flats were placed outdoors under shade cloth rather than in a greenhouse and were exposed to natural, diurnal temperature fluctuations. During the study, temperatures ranged from 28° C to 11° C. Relative light intensities (RLI) were controlled as above but lower light levels were included; relative values averaged 100%, 30%, 14%, 2% and 0.35%. Light intensity, measured at noon under open conditions, ranged from 230 to 2300 uE/m2.s1.

Role of feral pigs in germination and dispersal

A preliminary experiment suggested that the germination rate of Passiflora mollissima is increased by ingestion of seeds by feral pigs (Sus scrofa L.). A one-year old male pig weighing 80 pounds was captured in June of 1980 in Hawaii Volcanoes National Park. The animal was penned and fed a diet of coconuts for several days prior to the experiment until no seeds were found in the scats. The pig was then fed a diet of ripe P. mollissima fruit, collected at Laupahoehoe, for two successive days followed by a diet of coconuts for the next five days. The amount of fruit fed to the pig varied in each trial as follows;

1. one-half dozen fruit twice each day
2. one dozen fruit twice each day
3. two dozen fruit once each day.

Scats were examined until no seeds of P. mollissima remained. Seeds were collected from scats and a random subsample of 100 seeds was dried, measured and weighed. These weights and sizes were compared with an equal number of fresh seeds and seeds collected from wild pig scats.

Seeds from four sources: ripe fruit, dried seeds collected in November 1979, seeds collected from wild pig scats and seeds collected from captive pig scats, were planted in flats according to a random block design and placed in the greenhouse at Hawai'i Volcanoes National Park. Two replicates per treatment were used and the entire experiment was replicated twice. Germination, growth and survival were monitored for one year. After six months, flats were removed from the greenhouse and placed outside. Survival after one year was determined for each treatment.

Physiological Life Cycle

At each study site (same as those described in phenology) a set of 70 plants in three age classes was randomly selected and tagged in May 1980 and followed for 20 months. Initially, the basal diameter, height, vigor and life form of each individual was recorded. A shoot on each plant was selected and information on its basal diameter, number of nodes, leaves, and lateral branches, shoot length and condition of the apex was recorded. Lengths were measured either from the branch origin or from a permanent metal tag located some distance from the origin. Seedling height was measured from the ground surface. Growth rate was calculated as the increase in shoot length divided by the number of days between observations. The annual increase in shoot diameter was also monitored.

Individuals were monitored monthly and any changes in the above conditions were noted. Age classes were delimited as follows:

1. seedling--non-reproductive individual without tendrils
2. juvenile--non-reproductive individual with tendrils
3. adult--plant of reproductive age.

Those individuals added during the course of the study were not considered in mortality calculations.

Measurements of the Population Structure, Density and Cover

A count plot method (Mueller-Dombois and Ellenberg 1974) was used to determine the density and population structure of Passiflora mollissima at seven selected sites, located within the three major study areas, between June and August 1980 and 1981.

A belt transect was laid out through each population from a randomly-selected starting point in a predetermined compass direction. Contiguous 10 by 10 m plots were placed on both sides of the transect and the basal diameters of all individuals greater than 1 m tall were measured with vernier calipers. Plots were sampled until a minimum 30 individuals (if possible) in each of three predetermined height classes (< 1 m, 1-5 m, > 5 m) were enumerated. At site L3 the entire area (1500 m2) was sampled as a single plot as the area was small and homogenous and surrounded by a different vegetation type. The heights of these individuals were estimated based on known heights of selected trees (calculated with Abney level). An individual was delimited as all stems arising from a single above/below ground origin and its diameter equal to that of the thickest stem found. Only those individuals with more than 50% of their total basal area located in plots were counted.

For individuals less than 1 m tall, only heights were measured. In areas of high seedling density, 0.25 m2 subplots were randomly placed within the larger plots. The number of subplots necessary was determined by taking the running mean of the population (Mueller-Dombois and Ellenberg 1974).

Density counts of individuals greater than 1 m in height were divided into 5 mm diameter classes; those less than 1 m were divided into three height classes (≤ 0.1 m; 0.1 to 0.5 m and 0.5 to 1.0 m). All densities were extrapolated to a per hectare basis and plotted as histograms. The density of P. mollissima in each structural layer was also plotted in a histogram, for each site. In addition, estimates were made of the percent cover of P. mollissima in each structural layer of the forest as well as the total vegetation cover of each layer.

Reproductive Biology

Observations on floral movements and pollinator activity were made daily, on 20 tagged flowers, from August 25 to 28, The study site was located in an open, disturbed Metrosideros-Acacia forest 90 m north-northeast of the Keanakolu Ranger Station, at 1600 m on Mauna Kea (19° 55' 20" N. Lat./155° 20' 32" W. Long.). The relative position of all floral parts was recorded and photographed at representative stages each morning, afternoon and evening. Insect visitations and behavior were noted and specimens collected, if possible, for identification.

Pollination studies were conducted from January to March 1982 in an open, disturbed Metrosideros forest located behind the University of Hawai'i Agricultural Experiment Station Volcano Farm at 1240 m on Hawai'i. To assess the relative frequency and importance of natural autogamy and open pollination on fruit set, 250 mature buds were selected at random, tagged and assigned to one of the following five treatments:

1. Flowers intact; no bags
2. Flowers intact; bagged
3. Flowers hand-selfed; bagged
4. Anthers removed; flowers bagged
5. Stigmas removed; flowers bagged

Hand-pollinated flowers were emasculated in the bud before dehiscence, then bagged. Upon anthesis, a liberal amount of pollen was applied to each stigmatic lobe, using clean forceps, from the anthers of the nearest flower on the same plant. Anthers were removed prior to dehiscence and stigmatic surfaces prior to anthesis to check for the possibility of apomictic fruit set.

Pollination bags were made of Handi-wipes sewn up both sides, attached to the peduncle with flagging tape and stapled. To give bags rigidity and prevent them from pressing against flowers, a thin film of paraffin was applied to the lower third of each bag. Flowers were examined after three weeks and again at 10 weeks following pollination to determine the percent fruit set. The persistence and enlargement of the ovary with subsequent development of near-ripe fruit was used as the criterion for successful pollination. Fruit was examined for normal seed development but seeds were not germinated.

Phenology

The phenological behavior of Passiflora mollissima was monitored monthly in three representative areas from May 1980 to December 1981. The study areas included: Kaloko, 30 m east of Kaloko Rd. at 1460 m elevation (19° 43' 11" N. Lat./ 155° 55' 40" W. Long.); Laupahoehoe, 15 m east of Blair logging road at 1585 m elevation (19° 54' 34" N. Lat./155° 19' 40" W. Long.) and 'Ola'a, 0.8 km past the bend in Wright Rd. and 30 m east of the road (19° 28' 16" N. Lat./155° 15' 42" W. Long.). The second 'Ola'a site was located nearby, 0.6 km east-northeast of the bend in Wright Rd. (19° 28' 16" N. Lat./155°14' 46" W. Long.). Twenty reproductive individuals were randomly selected, tagged and monitored for the following characteristics:

1. vegetative flushing--conspicuous growth of shoots (including production of new nodes, leaves and flower buds)
2. flowering--all conspicuous stages of flowering prior to anthesis
3. anthesis--opened flowers
4. fruiting--mature, yellow fruit present

Entire plants were surveyed with binoculars for the presence and abundance of each phenophase.

The seasonality of growth and leaf turnover was monitored on a randomly-selected shoot on each individual. The following characteristics were measured monthly:

5. leaf turnover--change in number of leaves per shoot
6. shoot diameter change--change in basal diameter of each shoot, measured with vernier calipers
7. shoot length change--change in shoot length as measured from a standard reference point
8. internode expansion--growth divided by the averavge number of internodes per shoot

Data for the 'Ola'a site are incomplete for 1981 due to access problems: no data were collected for June and only one-half of the individuals were sampled in July. A new population of plants, tagged in August 1981, was sampled for the remainder of the study. Site characteristics were similar at both 'Ola'a sites, which were located less than one-quarter mile apart.

Quantification of Phenological Data

Due to the difficulty in accurately counting all flowering, flushing and fruiting branches on an individual vine, a phenological index similar to that used by Lamoureux (1973) and West & Wein (1971) was constructed to quantify monthly changes in flushing, flowering and fruiting. The following values were assigned, prior to monitoring, and represent the percentage of branches in each particular phenophase:

a. flushing-- 0 = none;
   1 = 0 to 25; 2 = $\geq$ 25 to 50; 3 = $\geq$ 50 to 75;
   4 = $\geq$ 75
b. flowering (including anthesis); fruiting-- 0 = none;
   1 = 0 to 15; 2 = $\geq$ 15 to 30; 3 = $\geq$ 30 to 45;
   4 = x $\geq$ 45

A cumulative site index for each month was constructed by summing the individual values and taking their arithmetic mean for each phenophase. Growth characteristics (#5-#8 above) were quantified directly and summed for each individual to give monthly values at each site. All negative growth recorded, due to the death of apices or small errors in measurement, was set to zero when calculating the mean growth rates.

Data Analysis

To determine the significance of each variable on germination rate and success, results were subjected to an analysis of variance using the SAS Anova Program on the IBM 370 computer at the University of Hawaii Computing Center. Duncan's Multiple Range test was used to determine which treatments were significantly different.

The mean growth rates of the shoot and its increase in diameter were calculated for each age class and site. Growth rates were subjected to an analysis of variance to determine if

any significant differences in growth rate occurred with age. The analysis was conducted using the SAS General Linear Regression model which performs an ANOVA on unbalanced data. Duncan's Multiple Range test was used to determine the significance of paired comparisons of means for each combination of age and site.

Mean monthly values for each phenophase were plotted against time of year. The presence of annual patterns in phenophases and climatic variables including total monthly rainfall, mean monthly air temperature and daylength at three sites in Hawai'i and three representative sites in South America was tested using a least-squares curve-fitting technique adapted by Dr. K. W. Bridges (Bridges et al. 1981). The data was transformed using the sine-based function $Y = a + b \sin((c + x)(2d-1))$ where a = mean value, b = amplitude, c = displacement of the curve (given as date of maximum response) and d = the fundamental period, which was set to 1 year. Pearson's correlation coefficient (r) provides an estimate of the goodness of fit of the data points to the sine-based curve; a value close to one indicates a good fit. This program, SINFIT, is available on the HP-2000 computer at the University of Hawaii at Manoa.

In addition, regression analysis was used in an attempt to relate the variations in monthly phenological activity to monthly climatic variations in both Hawaii and South America. The SAS RSQUARE program, available on the IBM 370 computer, tests all possible combinations of the dependent variable (phenophase) in the model with the given independent variables (climatic parameters), and prints an r-square value for each model tested.

Longterm mean monthly temperature data were obtained for the nearest currently-operable meteorological station at an equivalent elevation (State of Hawaii 1970). At Kaloko, a lapse rate of 5.4 °C per 1000 m was added to the temperature to adjust for the difference in elevation between the study site and the station. Longterm monthly total rainfall averages were from the nearest meteorological station (State of Hawaii 1970) and rainfall for 1980 and 1981 were obtained from the Division of Water and Land Development (DLNR), State of Hawaii. Longterm averages of mean monthly temperatures and total monthly rainfall at three South American sites, Bogota (Colombia), Quito (Ecuador) and Huancayo (Peru) were obtained from World Weather Records (US Dept. of Commerce 1959, 1966). Daylength data for Hawaii and South America were excerpted from Smithsonian Meteorolgical Tables (List 1966).

RESULTS

Germination and Dispersal

Seeds of Passiflora mollissima are 5.9 mm (± 0.1) long by 4.2 mm (± 0.07) wide and surrounded by an orange succulent aril. The ruminate seed coat is hard, thick and contains a dark brown

water-soluble substance. Mature embryos are small with two thin cotyledons and ruminate endosperm which occupies much of the area inside the seed at the time it is shed.

Although the germination rate increased following dry storage, there was no significant difference in rate between seeds stored for five months and those stored for one year (24.3 and 25.7 days respectively; p=0.05). Dried seeds remained viable for at least eighteen months under conditions of 20-25 ^{o} C and 50-60% relative humidity. Seeds planted in flats germinated as long as 8 months after sowing.

Germination success, following exposure to various light intensities, ranged from 17% to 78% after nine weeks (trial one) and from 34% to 45% after ten weeks (trial two) (Table 3). Within treatment variability was large and no significant differences in germination success were found under relative light intensities less than 33% (Table 3). No attempt was made to compare trials statistically as seed age and other environmental conditions were not equivalent for both experiments. The low value for germination success at 100% RLI at Volcano (1) (Table 3) was the result of soil desiccation late in the experiment rather than a direct result of high light intensity. When seeds were germinated under low light intensities (3.6% RLI) and high temperatures (40-50 ^{o} C), seedlings were highly susceptible to damping-off.

Germination rate showed a significant positive response to increased light intensity (Rate=0.02+(0.001 log(%RLI)); r2=0.85). The average number of days to 50% maximum germination increased from 40 days under full sun to 63 days under 0.35% light (Table 3); within treatment variations were small. Germination rates for relative light intensities between 2% and 100% of full sun were not significantly different, however (Table 3).

Increased temperatures associated with higher light intensities may have been at least partially responsible for the higher germination rates. The relationship of temperature and relative light intensity was linear (r2=0.969) over the narrow range of temperatures encountered (20-25 ^{o} C). In trial two, shaded flats were placed outside and average noon temperatures ranged from 20 ^{o} C, under 0.35% RLI, to 25.5 ^{o} C under full sun. Germination rates exhibited a positive, exponential relationship to temperature (Rate=0.07+(0.03 log(temp)); r2=0.611). Temperatures during the first experiment averaged 10-15 'C higher than normal due to greenhouse conditions.

Feral Pigs

During this study, seeds of Passiflora mollissima were frequently found in feral pig scats and occasionally in cattle droppings. Evidence of fruit eaten while on the vine and after falling to the ground was noted but no animals were observed eating P. mollissima fruit. When fed a restricted diet of

coconuts and P. mollissima fruit, length of the passage time through the pig increased with the amount of fruit eaten each day and the frequency of feedings. When the pig was fed one-half dozen fruit once a day for two days, passage time was complete within two days; with two dozen fruit once each day, passage time increased to three days and with one dozen fruit twice each day, seeds were passed for a total of five days. In all cases, 24 to 36 hours passed before seeds first appeared in scats. Passed seeds showed no difference in size (length 6.0 mm vs 5.9 mm; width 4.2 mm) or dry weight (Table 4) but those seeds collected from scats in the field were significantly lighter than controls. The mechanical removal of the aril from seeds had no significant effect on the germination rate ($p=0.05$); seeds with and without arils germinated in 49 days.

In a preliminary test, seeds collected from wild pig scats germinated significantly faster than stored, dried seeds. The experiment was later expanded to include fresh seeds, stored dried seeds, seeds from wild pig scats and seeds passsed through a captive feral pig. When all treatments were compared, seeds from captive pig scats had a significantly lower germination success than all other treatments (Table 4). Germination rate was equivalent for fresh seeds and seeds passed through the captive pig (30.3 and 70.3 days respectively) but these two treatments were significantly slower than stored, dried seeds and seeds from wild pig scats collected in the field (25.7 and 31.0 days respectively-no significant difference) (Table 4). The survival of seedlings over a one year period showed no significant difference ($p=0.05$) for any treatment.

Population Structure, Cover and Density Estimates

All seven sites generally contained a range of basal diameters (mature individuals) exhibiting only slight reductions in number with increasing diameter (Figs. 5-6). Bimodal distributions of diameter classes are found at sites O1 and L2 (Figs. 5,6); smaller gaps at sites K2, L1, L2 and O2 (Figs. 5,6) are possibly due to an insufficient sample size in these categories, however the sites were not resampled to determine if this was correct. The histograms presented in figures 5 to 6 represent densities extrapolated to a per hectare basis; actual counts of individuals in each diameter/height class are presented in Appendix 1.

The population structure of mature individuals was similar at both Kaloko sites in that basal diameters were skewed towards the smaller size classes; most individuals were less than 35 mm in diameter (Fig. 5). The two sites selected for study in the 'Ola'a Tract showed different population structures. Site O1 was characterized by a disjunct, bimodal distribution of diameter classes (Fig. 5). The largest diameter class was represented by a single individual within the study plots. Excluding this latter class, diameters were heavily skewed to lower values. Site O2 contained a wider, more continuous range of diameters, (O

to 40 mm) (Fig. 5). The pattern of densities was slightly irregular, however, decreasing with increasing size over most of the range (diameter) but increasing in the largest class.

Laupahoehoe sites exhibited the widest range of diameters of all three areas. Populations at sites L1 and L3 were composed of a fairly continuous, wide range of diameters (Fig. 6). In contrast to these sites, L2 exhibited a disjunct, bimodal distribution of diameter classes (Fig. 6) similar to that found at site 01 (Fig. 5). A large gap, represented by only two individuals within the study plots, occurred between the 0-40 mm diameter group and the 75-85 mm diameter group.

The population structure of the reproductive classes was one of two basic types; an inverse "J" exponential relationship, present at sites K2, L2 and L3, or one of small, essentially linear decreases with increasing size, present at the remaining sites. The structure of reproductive classes was somewhat irregular at sites K1 and 01; with a slightly greater density in one height class than the next lower class (Fig. 5). Reproductive classes exhibited a minimum of one-to-one replacement of mature individuals by the largest stem-length class (0.5-1.0 m) (Figs. 5,6), with the exception of site L1.

Reproduction was abundant at sites K2, L2 and L3 with densities ranging from 121,000 to 555,000 indiv. per ha. in the smallest size class. Density of this class was considerably less at site K1, 01, 02 and L1 with only 500 to 4700 indiv. per ha. (Table 5). In contrast, the density of "established " individuals (1.0 m tall) ranged from 780 to 5770 indiv. per ha.: a four-fold difference (Table 5). The highest density of established individuals was at site K1; the lowest at site L1 (Table 5).

The density of P. mollissima in various vegetation layers exhibited a similar trend at all sites; density generally decreased with increasing plant height (Figs. 7-9). Cover, however, was greatest at intermediate heights and decreased in both the understory and the emergent layer, as did total plant cover (Figs. 7-9). At site K1, vine cover was greatest in the T2 layer; total cover in the emergent layer (Fig. 7). Cover of Passiflora mollissima was generally less than 20% in all vegetation layers at all sites, except for site 01, where individuals had blanketed much of the vegetation in the area (Fig. 9).

Survival

Short-term survival was measured directly for the period of 13 months. During this time, 32% of all seedlings (68% mortality), 75% of all tagged juveniles (25% mortality) and 98% of all adults survived (2% mortality). The short-term survival of juveniles and adults differed little among sites; seedlings showed greater variability (Fig. 10). At all sites, survival was

greatest in adults: 100% of the tagged individuals survived at Kaloko and 'Ola'a while at Laupahoehoe, adult survival was 90%. Survival of juveniles ranged from 75% at Kaloko to 58% at 'Ola'a. Survival was lowest in the seedling stage. At Kaloko, 40% of all seedlings survived; survival was slightly less (30%) at 'Ola'a and lowest (25%) at Laupahoehoe (Fig. 10).

Long-term seedling survival may be estimated indirectly from population structure data by taking the difference between densites at selected stages in the life cycle. Of interest here are the following stages: germinant ($\leq$ 0.1 m tall), "establishment" (0.1- 1.0 m tall) and established indiviudals ($\geq$ 1.0 m tall). Estimates of the survival from the germinant to the "establishment" phase ranged from 0.3% to 127% (Table 5). Survival was high where the density of germinants was initially low. Likewise, survival was low where the initial density of germinants was high, such as sites K2, L1 and L2 (Table 5). Establishment (from "establishment" to established phases) was fairly high (40%) in all populations except at site K1 (24%) (Table 5).

Growth

Growth rates of seedlings averaged 0.07 cm per day (25.5 cm/yr) (Table 5). On the average, juveniles grew faster than either seedlings or reproductive individuals. Calculated growth rates of juveniles averaged 0.25 cm per day (92.0 cm/year). In some cases, growth exceeded 300 cm per year. Growth of reproductive individuals was variable, ranging from 0 to 0.71 cm per day on selected shoots. The average growth of adult shoots was 0.19 cm per day (67.9 cm/year) (Table 5). If all adult shoots are divided into 'flushing' and 'non-flushing' individuals, flushing shoots grew an average of 0.74 cm per day while non-flushing shoots grew only 0.08 cm per day, a highly significant difference (p=0.001).

The effect of age on the growth rate of P. mollissima differed at each site. Juvenile plants grew more rapidly in length than adults, at 'Ola'a and Laupahoehoe. At Kaloko, differences were not statistically significant (Table 7). Differences in growth between adult and juvenile plants occurred only at 'Ola'a (Table 7). Growth in height (increase in length and internode expansion) was significanlty slower in seedlings than in juvenile and adult shoots at all sites except 'Ola'a, where the differences in the daily increase in shoot length between seedlings and adult shoots were not significant (Table 7). The yearly increase in shoot diameter was greater in adults than juveniles, at all sites (Table 7).

At all stages in the life cycle, growth of shoots (increase in length) was most rapid at 'Ola'a and slowest at Kaloko (Table 7). Patterns of shoot diameter were opposite those of shoot length: significantly higher rates occured at Kaloko than at Laupahoehoe or 'Ola'a, for adult shoots (Table 7). In juveniles,

all sites exhibited significant but small differences in growth rates (diameter) (Table 7). The three stages in the life cycle also exhibited different periodicities in their growth patterns (Table 8; Fig. 11). Adults exhibited the greatest periodicity in shoot growth (r=0.768); juveniles the least (r=0.303; see results:phenology for explanation of periodicity function). All age groups experienced their peak of growth during the summer months but peak juvenile growth occurred in mid-June, two months before the peak in adult growth (mid-Aug). Seedlings were intermediate in their seasonality (r=0.569) and experienced a peak of growth in early July. Growth in shoot diameter was extremely variable from month to month and likewise exhibited a low seasonality coefficient (r=0.123, 0.258) in both juveniles and adults (Table 8).

Sixty percent of all juvenile and 56% of all adult shoots suffered injury to the apex, either physiological or biological, resulting in shoot-tip abortion. Most of these shoots later sprouted laterals but approximately 10% to 20% did not recover. Leaffall was asynchronous; an average of 1 leaf per shoot was lost during a six month observation period. During this same period, average leaf life, on reproductive individuals, was 4.4 months ($\pm$ 0.9 months). Average leaf turnover rates for individual shoots ranged from 18% to 30% per annum for the three sites.

Reproductive Biology

An average of 2.7 flower buds per branch were produced, over an 18-month period, on all tagged shoots and 5.2 flower buds on reproductive shoots. Anthesis occured approximately two months after bud initiation and lasted an average of three days.

Flowers of Passiflora mollissima are pendent. In the bud stage, anthers are introrse and held tightly against the androgynophore by pressure from the perianth. The styles are vertical, with stigmatic surfaces just below the level of the appressed anthers and directed downward (Fig. 12a). Dehiscence of the anthers usually occurs in the bud stage one to several days prior to anthesis.

Upon anthesis, the perianth separates, releasing the versatile anthers which rotate to a horizontal position, 90° from their original, downward orientation (Fig. 12b). At anthesis, the stigmatic surface is only slightly sticky and will retain some pollen, if applied, but becomes more viscid with time. The actual receptive period of the stigmas was not determined.

Later on the first day of anthesis, the perianth lobes continue to open, reaching a horizontal position, exposing the anthers (Fig. 12c) and stigmas. The anthers reflex further, becoming extrorse (Fig. 12d); later the styles begin to recurve upward and outward. In some cases, stigmas occasionally contact the anthers as they move by, transfering pollen.

Late in the first day or early in the second day, following the movements of the reproductive organs, the perianth reflexes further, and is oriented nearly 130° from its original position (Fig. 12e). No further movements of the reproductive organs occur until the third day when the flower begins to wilt; flower parts relax and return to their earlier downward orientation (Fig. 12f).

Highest fruit set occurred in hand-selfed flowers (Table 9). After, three weeks, 65% of hand-selfed flowers set fruit compared with 41% fruit-set in open-pollinated flowers. Natural selfing occurred at a very low frequency in this population. No apogamic fruit set occurred in flowers which had anthers or stigmas removed prior to anthesis. A high rate of abortion ocurred subsequent to initial fertilization; fruit set was lower after 10 weeks than after three weeks, in all cases. The extent of abortion varied with treatment (Table 9). Abortion in open-pollinated individuals was much higher than in hand-selfed. Two out of three fruit set following natural selfing later aborted.

An additional estimate of fruit abortion, on a wider scale, came from shoots monitored monthly for phenological observations at three sites. Over an 18-month period, fruit abortion ranged from 0% to 70% per shoot (average 28%). Fruit set on these same individuals, which are comparable to open-pollinated flowers in the controlled experiment, averaged 28%. An average of 1.6 fruit was produced on each reproductive shoot, the number for all shoots was somewhat lower, 0.95 fruit per branch.

The most frequent visitor to the flowers of Passiflora mollissima during August 25 to 28, 1981 was the honey bee (Apis mellifera L.) which was regularly observed collecting pollen. Flower flies were also frequent visitors. Allograpta obliqua Say, Toxomerus marginatus Say and Eristalis tenax L. were all observed feeding on pollen of P. mollissima. Individuals of T. marginatus were also observed transferring pollen from anthers to stigmas of the same flowers. Thrips (Thysanoptera) and Drosophila sp. were frequently encountered in flowers. The native butterfly Vanessa tameamea L. and the blowfly Calliphora sp. (probably C. megacephala (Fab.)) were occasional visitors to flowers.

Native and exotic forest birds, including the i'iwi (Vestaria coccinia (Forster)), amakihi (Loxops virens (Gmelin)), o'mao (Phaeornis obscura obscura (Gmelin)) and the exotic white eye (Zosterops japonica japonica Temminck & Schlega), were frequent visitors to flowers but were never observed approaching flowers from the corolla throat. Rather, these birds were repeatedly observed piercing the base of the hypanthium to obtain nectar. Similar behavior was also exhibited by the honey bee. A random survey of 100 flowers at Laupahoehoe, Kaloko and 'Ola'a, in 1981, revealed that an average of 52% of all flowers showed evidence of attack by nectar-seeking herbivores. Of these, 50%

were attacked by small herbivores, principally Hymenoptera; the rest were presumably attacked by birds (Fig. 13).

Flowers and fruit of Passiflora mollissima were atacked by a number of pathogens. Flowers were occasionally attacked by the grey mold Botrytis cinerea Pers. ex Fr. which resulted in flower abortion. The incidence of the mold was greater during wet periods. Fruits were frequently attacked by Alternaria passiflorae Simmonds and Alternaria sp., "brown -spot", and Colletotrichum sp., "anthracnose". Approximately 80% of all fruit in the 'Ola'a study area were infected to some degree. Fruit were also prone to cracking, resulting in poor fruit development or fruit abortion if cracked early in development.

Dimorphic flowers were noted at Laupahoehoe during July and August 1981. Normal flowers have long styles and large, well-developed stigmatic surfaces but approximately 20% to 30% of all flowers examined at this time had very short styles which never recurved, and rudimentary stigmas. Anthers were normal in both types of flowers.

Phenology: the Seasonality of Growth and Reproduction

Climatological and phenological data were subjected to a least-squares regression analysis utilizing a sine transformation. This function examines the annual periodicity in the data, based on a single annual peak period of activity. Pearson's correlation coefficient is used as an indicator of fitness of the data to the hypothetical curve. Bridges et al. (1981) have illustrated the utility of the sine-based function for examining the periodicity of phenological events in tropical species and climates.

This technique generally proved satisfactory for predicting the annual peak activity periods of reproductive phenophases but showed a poorer fit to growth characters. These latter characters tended to exhibit greater month-to-month variability rather than concentrated periods of high and low activity. The function also showed a better fit (more accurate prediction) for a mean index value (all sites combined) than for individual sites, where the observed peak may be as much as several months from the predicted one.

Flowering:budding

Flowering of Passiflora mollissima was continuous in Hawai'i, but generally exhibited a distinct annual periodicity as evidenced by the relatively high seasonality coefficient (r=0.73) (Fig. 14). Individual populations studied showed less seasonality (Fig. 15). Among these populations, Laupahoehoe was the most seasonal, Kaloko the least. A period of heightened bud production ocurred from May to August with a peak of activity estimated in mid-July (Fig. 14). Some variation was observed for individual populations. Based on the sine function, peak budding

occurred in mid-June at 'Ola'a, early July at Laupahoehoe and was delayed until early August at Kaloko (Fig. 15). The observed peaks coincided with the predicted ones except at Laupaheohoe, where it occured several months earlier (early May) than predicted. A small secondary peak occurred from November to December at Laupahoehoe and a less pronounced secondary peak period occurred during December and January at Kaloko. Overall activity (budding) was lowest at Kaloko and greatest at Laupahoehoe but site differences were not statistically different ($p=0.05$). More buds were produced in 1981 than the same period (July to Dec.) in 1980.

Flowering:anthesis

The peak of anthesis followed maximum budding by approximately three weeks and was less seasonal ($r=0.65$) (Fig. 14). Anthesis was fairly synchronized at Laupahoehoe and Kaloko (early Aug. and mid-Aug. peaks, respectively) but occurred three months earlier at 'Ola'a (Fig. 15). Laupahoehoe and 'Ola'a exhibited little seasonality in anthesis ($r=0.36$ and $r=0.33$) while Kaloko was slightly more seasonal ($r=0.52$). Overall there were fewer opened flowers at Kaloko than at either of the other sites ($p=0.05$).

Fruiting

Fruiting was also continuous and exhibited the greatest annual periodicity of any parameter measured ($r=0.92$). Heightened activity generally occurred between December and March with a peak in early January (Fig. 14). Peak activity was fairly synchronous in all populations, ocurring within a four week period between mid-December ('Ola'a) and mid-January (Kaloko) (Fig. 17). At Laupahoehoe, the observed peak was nearly two months later (late February) than that predicted. Laupehoehoe and Kaloko showed slightly less seasonality in fruiting ($r=0.79$ and 0.74 respectively). 'Ola'a exhibited a different fruiting pattern from the other sites. The annual seasonality coefficient was quite low ($r=0.29$) and there was little amplitudinal difference throughout the year ($b=0.145$) when compared with the other populations (Fig. 17). At 'Ola'a fruiting activity occurred in two short, slight, annual peaks from February to March and in September. Overall activity was significantly higher at Laupahoehoe ($p=0.05$).

Flushing

Flushing, accompanied by floral bud initiation, occurred throughout the year but exhibited a high degree of annual periodicity ($r=0.81$); the amplitude, however, was quite low ($b=0.312$). A sharp increase in activity occurred between April and June and the peak occured in early May (Fig. 14). The timing of this maximum was well synchronized: the observed peaks of activity occured in mid-May at all sites. Predicted peaks differed only slightly: mid-April for 'Ola'a and late April at

Laupahoehoe. At Kaloko, however, the peak activity was predicted for mid-June (Fig. 13). Individual populations had lower seasonality coefficients than the mean for Hawai'i (Figs. 14, 18). Kaloko was the least seasonal (r=0.649), while Laupahoehoe was the most seasonal (r=0.649) of sites. Little difference was found in the magnitude of activity among the three populations; they were not significant at the 95% level. Activity was generally lower in 1981 than the same period (July to Dec.) in 1980 with the exception of 'Ola'a, where 1981 exhibited greater activity.

Estimates of flushing activity based on an average of all branches on an individual and for a selected branch per individual gave very similar estimates of activity (Fig. 19), indicating that either method is satisfactory for constructing a phenological index. On the other hand, reproductive characters on individual branches were too few in number to adequately predict activity, on the basis of a sample size of 20. Estimates of the activity of the entire individual provided a more satisfactory result with the same sample size.

Growth

Growth rates, expressed as the daily increase in shoot length, were reasonably periodic, with a coefficient of r=0.77. Heightened activity generally occurred from June to September with a peak in early June, but individual populations showed considerable variation in growth rates from month to month (Fig. 14). The predicted peak for all sites combined was delayed until mid-Aug (Fig. 20). The 'Ola'a population exhibited the most seasonality (r=0.79) with the least variability (b =0.117) and also the highest growth rates (0.207 cm per day). The period of heightened activity was longest at this site, from June to October, and maximum growth occured in early October. When compared with 'Ola'a, Laupahoehoe and Kaloko exhibited less seasonality of growth (r=0.652 and 0.743, respectively) and protracted periods of elevated activity: June to August at Laupahoehoe and June to early August at Kaloko. Peak growth rates were fairly synchronous at these two sites, ocurring within a four week period (early July at Laupahoehoe and early August at Kaloko) (Fig. 20). The average growth rate at Laupahoehoe was 0.149 cm per day and at Kaloko, 0.117 cm per day.

Increase in shoot diameter exhibited the lowest degree of seasonality, in all populations, of any parameter measured (r=0.26) (Figs. 14, 21), but exhibited much greater month to month variation (Fig. 14).

Leaf Turnover Rate

Leaffall and production were estimated indirectly as the net change in leaf number per month. Passiflora mollissima is an evergreen species, however the leaf turnover rate per month exhibited a degree of seasonality (r=0.64). Net gain of leaves

occured in early January (predicted: late February) but the turnover rate was only 17% per annum (Fig. 14). Within individual populations, there were differences in both seasonality and magnitude of turnover (Fig. 22). At 'Ola'a, turnover was highly seasonal (r=0.94) with the greatest gain in February (predicted: March) and the lowest number of leaves per shoot occurring in late September: the annual turnover rate was 27%. Kaloko exhibited a similarly high turnover rate, 30% per annum, but seasonality was nearly opposite: the greatest number of leaves per shoot occurred in January while the lowest number was found in April. Laupahoehoe experienced a considerably lower annual turnover rate, 18% per annum, and leaffall and production maxima occurred between the dates reported for the other two sites (Fig. 22).

Association of phenological cycles with climatic trends

A stepwise regression technique was used to determine which climatic variable, temperature, daylength or rainfall, best explained the observed variation in each phenological index. The value of each climatic parameter was also subjected to a lag of 1, 2 and 3 months and compared with the phenological index. Results of these regressions (Table 10) suggest that climate in Hawaii had little effect on the phenology of P. mollissima; r-square values were less than 0.57 in all cases and there was no general agreement among sites. The high degree of significance (probabilities equal to or greater than 95% in all but 2 cases and often equal to 99.9%) for most of these regressions indicates that there is a relationship between variables. For example, as rainfall increased at Kaloko there was a simultaneous increase in flushing activity. However, the low r-square value (0.46) indicates that little of the variation in flushing was explained by the variation in rainfall. When phenological activity in Hawaii is compared with climatic parameters at three representative sites in South America, a very significant correlation occurs between daylength at Huancayo, Peru (10' S Lat.) and flushing activity three months later in Hawaii. This relationship also has a very high r-square value: 0.99. Flushing activity, however, showed very little relationship to the variation in daylength in Hawai'i (r^2 = 0.1). No other combination of variables produced an r-square greater than 0.5, although several other relationships were significant (Table 10). The addition of variables to each model did little to improve the r-square value of any model and these are not reported.

DISCUSSION

The Physiological Life Cycle of *Passiflora mollissima*

Seed Germination and Dispersal

Seed germination in *Passiflora mollissima* is staggered ("intermediate" sensu Ng 1973). Seeds are shed in a dormant state and require a short period of afterripening prior to germination. The minimum period is unknown, but in this study, seeds generally began to germinate four to twelve weeks after planting; dry storage reduced this period to 2 weeks. Once dormancy is broken, germination within a cohort is fairly rapid and synchronous; most seeds germinate within eight weeks. Some seeds may retain viability in the soil and germinate at least eight months after sowing. Dried seeds retain their viability for at least eighteen months.

Escobar (1980) reported a similar delay in germination and an increase in the germination rate with seed storage. All nine species of *Passiflora* (*Tacsonia*) planted germinated within 15 days, after 4 to 12 months of storage; one year old *P. mollissima* seeds within 9 days (Escobar 1980). In contrast, seeds of *P. triane* Killip, planted within one month of collection, did not germinate for three months. Other published reports indicate longer lag periods, from five weeks to 20 weeks (Jaramillo 1953; Schoniger 1969). The age and condition of the seed are not specified in these latter experiments therefore it is impossible to determine if this difference represents an inherent variability or results from environmental factors. Seed dormancy may be due to one or several innate factors: the presence of a hard, lignified and heavily cuticularized seed coat (Dathan & Singh 1973) and/or an immature embryo, as suggested by Escobar (1980). No other references to delayed embryo development in *Passiflora* spp. were found, however the embryology of very few species has been investigated. Retention of apparently-ripe fruit on the vine, for several weeks, may be a mechanism to allow further embryo development before the fruit is shed.

Staggered germination and an enforced period of afterripening, coupled with a hard, impervious seed coat, are clearly adaptive in the case of animal dispersal, which is known from Hawai'i and supsected in the native range. Seed dormancy and staggered germination may also be adaptive in gap-phase replacement. Most tropical seeds possess no dormancy mechanism (Ng 1973; 1975) but delayed germination occurs in a small number of species. Afterripening was noted in *Morrenia odorata* Lindl., a weedy vine from South Florida (El Ghol et al. 1979) and the native gap-phase tree, *Palicouria riparia* Benth., from Puerto Rico (Lebron 1979).

Light does not limit germination of *P. mollissima* in most Hawaiian forests. Germination rates increase with light intensity but are only significantly inhibited at light

intensities less than 2.0% full sun (Table 3). Germination success is not related to light intensity. Low light levels found in Cibotium forests (Burton and Meuller-Dombois in press) may decrease germination rates but do not limit the establishment of P. mollissima (LaRosa 1982).

It is not entirely clear whether the enhanced germination rates in high light intensities are the result of light or the higher temperatures associated with increased intensity. Light may affect germination by breaking seed dormancy (induce afterripening). Although not strictly a temperature-dependent process, germination rates often increases with temperature, up to a species-dependent threshhold (Mayer and Poljakoff-Mayber 1975). Elevated temperatures associated with high light intensities may result in soil desiccation. In areas with insufficient soil moisture, these conditions may be detrimental to the survival of P. mollissima and counteract the benefits of higher germination rate with lowered success (Table 3). While both temperature and light intensity are related to germination rate, light shows a stronger correlation to observed germination rates than does temperature (r^2=0.85; 0.61, respectively). Further experiments are necessary to determine the exact nature of the relationship between temperature, light intensity and the rate of germination.

Continuous, prolific fruiting of P. mollissima in Hawai'i provides abundant food for native and exotic birds and exotic mammals: more than 20 species are suspected of dispersing the seeds throughout the forest (Warshauer et al. 1983). Although feral pigs had previously been identified as principal dispersal agents (Wong 1971; Giffin 1972), their role in germination was largely unknown.

Experimental results (Table 4) indicate that feral pigs function principally as dissemination agents, evacuating seeds in a pulp-free condition one to five days after ingestion, which results in peripheral range expansion of P. mollissima. The distance to which pigs disperse seeds is probably limited chiefly by the size of their home range rather than the length of time in the gut. No enhancement of germination was noted following pig digestion (Table 4); the reason for the significantly lower germination success of seeds fed to the captive feral pig is unclear. The apparent discrepancy between the results of seeds collected from captive pig scats and those collected in the field may be due to differences in the stage of afterripening between the two treatments; the age of field-collected seeds was not known. Also, it is not clear whether the significant decrease in dry weight noted for seeds collected in the field from pig scats was due to the digestion of the seed coat by pigs or soil-borne and coprophilous fungi.

Although the passage of seeds through feral pigs does not directly increase germination, they frequently provide a fertile medium for seedling growth in the early stages of establishment.

This is further aided by rooting activities of pigs which create an environment with low competition. Seedlings of P. mollissima rapidly colonize these disturbed areas, which exhibit much higher densities than surrounding areas. Reduced competition is particularly beneficial where grasses form a dense ground cover. With repeated rooting of an area, however, many seedlings are subsequently trampled and/or uprooted.

Birds aid in the dispersal of P. mollissima to previously uninfested areas. In several instances, solitary seedlings were found in remote areas with no seeds or fragments in evidence and no reproductive individuals nearby. The largest nearest-neighbor distance measured in such areas was 50 m, but estimates of 1.0 km are common in densely vegetated areas.

Growth and Establishment Phases

The seedling stage is often limiting in the life cycle of plants; the phase in which greatest mortality occurs (Maruta 1976; Harper 1977). The extremely high density of germinants under most conditions is evidence that site conditions do not generally limit germination (Table 5). Seedling (germinants) densities are high near the parent vine and locally in areas with abundant pig activity. In other areas, individuals are widely scattered throughout the forest. The highest mortality occurs later, between the germinant and establishment (juvenile) stages (Table 5; Figs. 5-6). The survival of germinants to the juvenile stage is inversely proportional to their initial density (Table 5). While the density of germinants varies widely from population to population, the density of juveniles ("establishment"; Table 5) is more constant.

Seedlings are rooted in a variety of substrates from relatively unweathered 'a'a lava to deep, organic ash soils. A majority of the fibrous roots are located in the top ten cm of soil. Most seedlings appear vigorous and free of pests, except for slugs. In wetter areas, these animals frequently attack the growing tip, resulting in the eventual death of seedlings. Deep shade further reduces seedling survival by increasing their susceptibility to soil-borne fungi. Overall seedling survival during the 13-month period was fairly high (32%) and agrees with an independent estimate (average) from population structure analysis (40%).

Growth rates vary widely within populations but are generally characteristic of each stage of the life cycle (Table 6). At Kaloko, however, where the overall growth rates are lower, no significant difference occurs between the average growth rates of the rapidly-growing juvenile stage and the adult stage (Table 7). Average seedling growth in the field is 25 cm per year but some seedlings may grow one meter in their first year (Table 6). Others appear stunted and exhibit little or no growth and low vigor. Although most of these "arrested" seedlings succumb within the first year, a small percentage

survive. Seedlings grown under controlled conditions exhibited more uniform vigor, suggesting that differences in vigor are largely phenotypic.

Juveniles grow rapidly; under favorable conditions individuals commonly increase one to three meters in length in a single year, quickly reaching the canopy. Short-term survival of juveniles is very high (75%) and approximately 50% of juveniles survive to adults, based on estimates from population structure (Table 5).

A distinctive shoot morphology is found in juveniles and rapidly-growing (flushing) mature shoots and is likely a result of their rapid growth rates. In these shoots, leaves are sharply lanceolate and deeply lobed and internodes are long and flexible, as are tendrils (Fig. 23). Root systems of juveniles are still principally fibrous and superficial.

Growth rates of adult shoots are variable and composed of two discrete phases, each with characteristic growth rates. Growth of flushing shoots exceeds that of non-flushing shoots by a factor of 10 and is three times faster than average juvenile growth. Non-flushing shoots grow at a rate equivalent to seedlings. Enhanced reproduction usually accompanies rapid growth on flushing shoots, which are more common in the canopy and other areas of high light intensity. This proliferation is common in tropical lianas (Richards 1952; Brender 1961; Janzen 1971; Choudhury 1972), but a dependence upon light has not been systematically investigated.

The success of vines is commonly attributed to their rapid growth rate, but this assumption is largely based upon casual observation and inferences from population structure: little precise information on growth rates exists. Calculated growth rates (height) of P. mollissima are within the wide range of estimates for lowland tropical climbers (1 to 50 m/year), both herbaceous and woody (Bailey 1944; Janzen 1971; Choudhury 1972), and on a par with the tropical (lowland) pioneer tree Trema micrantha (L.) Blume (Ewel 1980).

In Cibotium forests, where light is at a minimum, individuals can overtop the canopy (commonly at a height of 3 to 6 m) in one to six years, if light is not limiting. Individuals may go from seed to reproductive maturity in a single year (Chapter 4). Gap formation aids this process and is discussed more fully in Chapter 4. Rapid growth rates were confirmed by Burton (pers. comm.). He noted that under favorable conditions following disturbance, P. mollissima attained the canopy (tree-fern) and reproduced in 14 months.

Adults of P. mollissima are typically climbing but may remain shrubby or become trailing when supports are lacking. Under conditions of high light intensity, shoots commonly retain most of their leaves, while they are shed under shaded

conditions. Sun leaves (also in dry areas) characteristically have a thicker indument (lower surface) while shade leaves and those in mesic areas are more sparsely pubescent. In large, mature individuals, a taproot is formed.

Shoot-tip abortion is a regular feature of P. mollissima; over half of all tagged shoots aborted during 18 months of observation. This condition appears to be largely physiological and most shoots (90%) sprout healthly laterals. This situation is also reported for Syringa vulgaris L. (Garrison and Wetmore 1961) and may be summarized as follows:

1. Shoot-tip abortion begins as cessation of apical growth.
2. The aborted shoot can be stimulated to regrow but regrowth is limited to vigorous shoots.
3. Delay or failure of shoot-tip abortion is associated with vigorous growth.

Survival and Senescence

Short-term survival records, estimates of long-term survival from population structure (Table 5) and a general paucity of senescent individuals indicates that survival rates of mature P. mollissima are very high. The life span is unknown but the population at 'Ola'a is more than 20 years old and possesses few senescent individuals. Schoniger (1969) estimated the life span of vines in South America at 15 years.

Pollination and Reproductive Biology

Complex movements of the reproductive organs are common in the genus Passiflora. Depending upon the species in question, these movements have been reported to promote allogamy, autogamy or both (Masters 1871; Foerste 1884; Raju 1954; Cox 1957; Janzen 1968; Hardin et al. 1972; Corbet and Willmer 1980; Escobar 1980).

The reproductive pattern of P. mollissima takes advantage of both autogamy and allogamy. As in most self-compatable species in the genus, protandry and the orientation and spatial separation of anthers and stigmas promote outcrossing during early anthesis. Later, stigmas become more viscid and pollen is still viable. Stigmas move to a position near the anthers permitting selfing (Fig. 12). Contact between anthers and stigmas of the same flower, with transfer of pollen, was observed on several occasions.

The high incidence of fruit set in hand-selfed flowers indicates that P. mollissima has a high degree of self compatibility. Results of pollination experiments further suggest that while autogamy is possible, it occurs in low frequency in the absence of a pollinator (Table 9). Exotic insects appear to be the principal pollinators of P. mollissima in Hawai'i. Generalist pollinators, including honey bees, and several members of the Syrphidae (flower flies), were the most

frequent visitors to flowers. Honey bees increase fruit set of P. mollissima in plantations in South America (Anon. 1962; Escobar 1980). Although thrips (Thysanoptera) and fruit flies (Drosophila) are commonly found in flowers, they are considered too small to be effective pollinators (Nishida 1963).

Long-billed hummingbirds, common in the high-elevation Andes, are suspected to be the indigenous pollinators of P. mollisima. Although long-billed nectivores occur in Hawai'i (Drepaniidae), their bills are of insufficient length to reach the base of the long floral tube and gain nectar directly. Although several birds, both native and exotic, regularly visit flowers of P. mollissima in Hawaiian forests, they function solely as nectar-robbers and do not appear to be involved in pollination. The herbivory on flowers by birds and insects does not prevent pollination and fruit set but the cost of nectar loss to overall reproductive success is unknown.

The prevalence of sunny weather during the experimental anthesis period is assumed to have resulted in near maximal levels of pollinator activity at this site. Pollinator efficiency, calculated as the difference between fruit set in hand-pollinated (maximal fruit set) and open-pollinated flowers was initially fairly high (65%), however many of the open-pollinated flowers subsequently aborted (Table 9). If early abortion is considered a result of insufficient pollination, and there is evidence that this is so (Akamine and Girolami 1959), then pollinator success later declined to only 30%. The relative contribution of autogamy and allogamy was not studied in this experiment but the results of three preliminary tests all showed a 50% higher fruit set in deliberately-selfed flowers when compared with crosses (deliberate).

The results of pollination experiments are generally in agreement with those of Escobar (1980), who studied the pollination of P. mollissima in South America. Fruit set was always higher in Hawai'i. Pemberton (pers. comm.), noted that fruit are considerably more abundant in Hawai'i than South America but the lower number may be a result of predation or other factors, rather than a consequence of pollination.

Fruit of P. mollissima ripen in 2.5 to 3 months and may persist on the vine for several weeks to more than a month. Several pathogens attack fruit while on the vine. Lesions of Alternaria spp. and Coletotrichum sp. occurred on 80% of all fruit in the 'Ola'a area in early 1982, but these fungi are not considered harmful to fruit development in Hawai'i (Aragaki pers. comm.; Hodges pers. comm.). Both genera are considered limiting factors in fruit production in South America (Jaramillo 1958; Schoniger 1969) but this may be for cosmetic reasons only.

Fruit are also susceptible to cracking although the etiology of this condition is unknown. If cracking occurs early in development, fruits remain small, seeds do not develop fully and

abortion commonly results. Approximately 40% of all fruit in the 'Ola'a study area were affected in early 1982. Fruit cracking may occur as a result of several factors. During a drought period, fruit growth is retarded and pericarp cell walls may become rigid. If a sudden rain follows, fruit swell rapidly and crack under the pressure. Such a period of drought followed by heavy rain occurred in the early part of 1982 and may have resulted in the high incidence of this condition. Fruit-split is also reported from South America where it results in the loss of 25% to 60% of an entire fruit crop (Anon 1962; Schoniger 1969). Flowers of P. mollissima are susceptible to attack by the gray mold Botrytis cineria Pers. ex Fr. which occasionally infects flowers, resulting in their subsequent abortion; the incidence of this mold increases during wet weather.

Dimorphic flowers were noted at Laupahoehoe during July and August 1981. While normal flowers, with long styles and large stigmatic surfaces, were most common, approximately 20% to 30% of all flowers examined at this time had short styles with rudimentary stigmas which remained below the level of the anthers at all times. In a majority of these flowers anther development was normal. These flowers appear to be functionally male but no attempt was made to monitor floral movements in these individuals or their subsequent fruit set. This phemenon was not recorded again and its incidence within this population and others in Hawai'i is unknown. Only a single reference to functionally dioecious flowers in the genus Passiflora was found. Akamine and Girolami (1959) reported that in some individuals of P. edulis f. flavicarpa in Hawai'i, styles remained upright and never recurved. These flowers never set fruit, even when hand pollinated.

Asexual reproduction contributes little to the reproductive effort of P. mollissima in Hawai'i. Apomictic fruit set does not occur. Occasionally, adventitous roots arise from nodes in areas where stems trail along moist soil or humus but few plants reproduce in this manner.

Periodicity in the Growth and Reproduction of Passiflora mollissima in Hawai'i

Many tropical moist forests have equable climates only when compared with temperate counterparts. Often rainfall, daylength temperature and asociated factors exhibit fairly regular annual patterns, cycling at low amplitudes, but sufficient to trigger the seasonal behavior of many tropical forest species (Janzen 1967; Walter 1971; Daubenmire 1972; Wycherly 1973; Opler et al. 1975; Stiles 1977). While tropical moist forest communities as a whole exhibit no marked seasonality of growth or reproduction, many component species exhibit periodic behavior (Janzen 1967; Croat 1975; Opler et al. 1980).

Due to the extensive altitudinal and latitudunal range of Passiflora mollissima in South America, populations are exposed

to a variety of climates. All sites can be characterized as cool, tropical montane environments with fairly even temperatures all year and a diurnal temperature range in excess of the annual variation. High relative humidity and regular periods of fog make significant contributions to precipitation in the montane cloud forests but P. mollissima is also found (perhaps only as an escape from cultivation) in the drier altiplano regions of the high Andes.

With respect to climate, populations studied in Hawai'i are generally within the limits found at most South American sites: the two regions differ principally in the duration and intensity of their dry periods. Differences in the seasonality of rainfall may be found within each region but in Hawai'i, periods of dry weather generally coincide with increasing temperatures and daylengths while in South America, the opposite is true (Table 11; Fig. 24). Daylength exhibits less amplitudinal difference in South America than Hawai'i but seasonality is opposite in southern and northern hemispheres.

Collectively, Hawaiian sites have higher annual precipitation and shorter, less pronounced dry seasons than selected South American sites (Table 11; Fig. 24). Both Quito (Ecuador) and Huancayo (Peru) experience annual periods of climatic drought, but drought is infrequent at Hawaiian sites. When fitted to the annual seasonality (sine) function, rainfall and temperature at South American sites have lower correlation coefficients than Hawai'i, suggesting a less seasonal environment (Table 12). Temperature and daylength exhibit seasonal patterns, cycling at low amplitudes, at all sites except Quito, an equatorial site (Table 12). Rainfall is less seasonal than daylength and temperature but exhibits a much greater yearly amplitude. A dry period of varying length and magnitude occurs at all sites. The low correlation for rainfall at Bogota, Colombia is the result of the presence of two, distinct dry periods annually; therefore the sine function is a poor fit. Although climate diagrams (after Walter et al. 1975) suggest that no effective dry seasons are regularly found at Hawaiian sites (Fig. 4), Janzen (1967) has noted that an effective dry season, with recognizable behavioral responses in resident organisms, is often defined by the relative differences in monthly rainfall rather than the absolute amount recieved. Some areas with effective dry seasons may receive as much as 150 mm of rain per month during the "dry season".

Populations and individuals of P. mollissima are asynchronous, exhibiting continuous growth and reproduction all year. Intraspecific and individual variation in phenological behavior is common in tropical species (Richards 1952; Daubenmire 1972; Lamoureux 1973; Frankie 1975; Opler et al. 1975). Seasonal differences in behavior are reflected in the relative magnitude of activity throughout the year. In general, elevated levels of various reproductive phases were concentrated into a single annual period, characterized by a gradual increase and decrease

(Fig. 14). Growth characteristics, although seasonal in nature, exhibit more frequent and shorter oscillatory periods. Diameter growth is not seasonal.

Differences in the phenological behavior of P. mollissima at each site were principally quantitative (magnitude of activity). In most cases, elevated periods of activity showed overlap among sites but the occurence of the absolute maxima often differed by one week to several months. Differences also occured in the amplitude of fluctuations among sites. 'Ola'a most frequently exhibited lower amplitudinal oscillations in reproduction, while yearly difference were greatest at Laupahoehoe. Greatest overall reproductive activity was generally found at Laupahoehoe; greatest growth rates at 'Ola'a. Qualitatively, phenological and climatic patterns showed greater similarities at the more mesic sites, 'Ola'a and Laupahoehoe, than either site showed with Kaloko.

A comparison of data from the second half of 1980 and 1981 reveals slight differences in the timing and magnitude of peak activity. Yearly variability is commonly reported for tropical species, particularly those growing outside pronounced seasonal habitats (Richards 1952; Daubenmire 1972; Croat 1975; Walter et al. 1975; Opler al. 1980). This inherent variability necessitates a minimum observation period of several years before phenological patterns can be predicted with accuracy. Therefore, conclusions reached from the current study must be considered preliminary, although they may be confirmed with further research.

A similar conclusion can be reached regarding the association of phenological behavior with climatic patterns. Climatic cues may be more sensitive than when expressed as longterm monthly averages and hence, overlooked in the analysis. Furthermore, during the majority of the study period (1980-1981), abnormal weather conditions prevailed (Appendix 2). In the early part of 1980, all sites experienced from one to two months of heavy rainfall (1-3 times average). Following this, rainfall was frequently well below average at Laupahoehoe and 'Ola'a. At Kaloko, rainfall was less than half of the average rainfall for five successive months during 1981 and a period of climatic drought occurred (Appendix 2). No wet period (100 mm rain per month) occurred at Kaloko between April 1980 and December 1981. Conditions accompanying lowered rainfall, fewer and shorter periods of fog and higher effective temperatures, added to the evaporation potential at all sites making them effectively drier than normal.

All phases of flowering (as observed in Hawai'i), from bud initiation (accompanying flushing) to anthesis, are concentrated in the dry season of all sites in Hawaii and South America (Fig. 24). Peak flushing occurs early in the dry season, (early May) and peak anthesis occurs in the mid-to-late dry season (early Aug.). When the patterns of individual populations in Hawai'i

are compared, two generalizations can be made. First, the delay in activity at Kaloko coresponds to a lag in the dry season found at this site (Fig. 14). Peak flowering (budding) does not occur in the relatively wet months of April and May but is delayed until June, when rainfall is declining. Second, there is a relationship between total annual rainfall at each site and the time between predicted peak phases of flowering activity (flush, budding and anthesis): these events tend to converge with decreasing annual rainfall (Fig. 24).

Peak flowering periods in Hawai'i are similar to those reported from South America, where activity is greatest from June through August (Herklots 1976; Escobar 1980). This is also the dry season in these areas (Fig. 24). Herklots (1976) also reports that maximum flowering occurs during the "summer months" in North Africa (Kenya). The preponderence of dry season flowering is widespread and well-documented for many areas in both the old and new world tropics, but the stimuli for this activity are little understood (Koelmeyer 1959; Snow 1965; Janzen 1967; Daubenmire 1972; Burger 1974; Opler et al. 1976; Stiles 1977; Jackson 1978). Climbing species studied to date, including Passiflora spp., characteristically flower during the drier season (Janzen 1967, 1968; Croat 1975; Benson 1978; Escobar 1980). Croat (1975) hypothesized that water stress, which may be particularly acute in climbing species, could be responsible for triggering flowering in those species during the dry season.

Cues for flower bud initiation and anthesis in tropical species may be similar to those in temperate areas, including photoperiod and thermoperiod, but cycle at a lower amplitude. Other triggers appear to be unique to tropical systems (Richards 1952; Koelmeyer 1959; Wycherly 1973; Stiles 1977; Opler et al. 1980). Stiles (1977) and Opler et al. (1980) proposed that the sudden drop in temperature (or increased humidity) regularly acompanying tropical summer storms is sufficient to trigger anthesis in certain species. This hypothesis accounts for the observed variability in the timing of phenological peaks of many tropical species: photoperiodic or thermoperiodic cues would likely result in more strictly defined annual peaks.

The common climatic variable, with respect to peak flowering periods, in all habitats of P. mollissima examined, is a period of low rainfall (Fig. 24). This trend, however, is not supported by a strong correlation between monthly rainfall and observed phenological patterns (Table 12). Other variables, including temperature and daylength exhibit variability in degree and seasonality among the sites. A very strong correlation (r^2=0.99) was found between daylength at Huancayo, Peru (putative species' origin) and flower bud initiation three months later in Hawai'i (Table 12) but the opposing seasonalities of daylength at various sites versus the constancy of flowering at all sites belies any cause and effect relationship. Furthermore, very low correlations (r^2 = 0.1) were found between daylength in Hawai'i and phenological behavior.

Little precise information is available on the variability of flowering periods throughout the native range of P. mollissima. The general similarity in phenological patterns at three sites in Hawai'i with differing seasonality and the agreement between the flowering and fruiting period observed for Hawai'i and those of South America and South Africa, strongly suggest an internal physiological ryhthm. Variations observed among Hawaiian populations may represent phenotypic plasticity or be a result of the physiological condition of the individual. The low correlation between environmental factors and phenological patterns (Table 12) and lack of agreement among areas, further supports this hypothesis.

While the mechanism responsible for the regular annual sequence of dry season flowering is little understood, the selective advantage of dry season flowering is more apparent. Plants of tropical regions depend heavily on biotic agents for their pollination, and a selective advantage is given to those species able to flower in the dry season. The close association between flowering seasonality and pollinator activity has been demonstrated for several groups of species in the tropics, including Passiflora spp. (Janzen 1967,1968; Gentry 1974; Frankie 1975; Stiles 1977). Insect activity (both diurnal and nocturnal) increases during the dry season and birds may seek out nectar to increase their daily fluid consumption (Janzen 1967,1968). In addition, heavy rains may be physically damaging to flowers and reduce pollen viability. Most Passiflora spp., including P. mollissima have large showy flowers adapted to pollination by insects or birds and occur in habitats where dry season flowering offers a selective advantage. This is also true of the introduced habitats of this species in Hawai'i, although little is known about the pollinating agents in Hawai'i or elsewhere.

In addition, solar insolation is greater in the dry season and this factor may be particularly important in areas of regular, heavy cloud cover, such as in Passiflora mollissima habitats. The increased light intensity may the stimulus for increased flowering during this period. The association between proliferation of climbing species and high light intensity has been noted previously.

Ripe fruit are produced in abundance during the winter, wet season (Dec. to Mar.) in Hawai'i. All sites show a similar duration of heightened activity. Peak fruiting is fairly synchronized among the sites (Fig. 17) but monthly variability (amplitude) is considerably lower at the wettest site, 'Ola'a. Maximum fruit production occurs at Laupahoehoe, a mesic site. Fruiting is continuous in South America (Escobar 1980) but the seasonality (magnitude), if any, is unknown. As fruit mature in approximately 3 months from the time of anthesis, it is apparent that peak fruiting is not strictly correlated with peak flowering. The reason for this is unclear at this time.

All measures of growth exhibit greater month to month variability than reproductive characters except for diameter growth, which is aseasonal (Fig. 14). The lack of seasonality may be a result of inadequate measuring techniques, as monthly changes were generally negligable. Higher growth rates occur during the warmer, drier summer months, but this is no doubt correlated with the stimulation of growth on flushing shoots. In contrast, Benson (1976) noted that lowland Passiflora spp. suffered large reductions in growth rates, in seasonal environments at Rio de Janeiro, Brazil (350 m annual rainfall) and these reductions occurred during the cooler, drier months of winter. No seasonal variation in growth was noted when these same species were grown in constant environments. Although P. mollissima is evergreen, there is some seasonality in leaf turnover during the year (Fig. 22). The lowest number of leaves is supported in the dry season while average number increases in the winter, wet season.

Population Ecology

Passiflora mollissima is established and successfully reproducing in a range of habitats in Hawai'i. All populations sampled were stable, exhibiting a range of sizes (diameters) of mature individuals, and self-maintaining, with active replacement of mature individuals by the reproductive classes. The bimodal distribution of diameter classes (mature individuals) at Laupahoehoe (3) and 'Ola'a (1) may represent a history of periodic perturbations resulting in successive waves of estasblishment or, more likely, a long establishment phase of the original immigrant(s).

Reproduction is abundant at most sites. Densities fall into two discrete categories: low to intermediate (5,000 germinants/ha.) and very high (120,000 germinants/ha.) (Table 5). Those populations with extremely high germinant densities (Laupahoehoe 2 and 3 and Kaloko 2) concommitantly have high densities and levels of feral pig activity. Germinants (and seedlings) suffer severe competition from exotic grasses which form a nearly-continuous ground cover at sites Kaloko (2) and Laupahoehoe (2). Young plants are generally densely clustered in areas of pig-rooting where competition from the grasses has been greatly reduced. Densities at these latter sites are less than one-half that found at Laupahoehoe (3), where ground cover is low (Figs. 7-8). Populations with low to intermediate germinant densities were found in areas of lesser pig activity, high canopy cover (Laupahoehoe 1; Kaloko 1), and in the case of populations in 'Ola'a, more recent invasion.

Vine cover and/or density is generally inversely proportional to the total plant cover at each site. Density of P. mollissima generally decreases with increasing height of the vegetation strata, as expected, but cover is greatest in the stratum immediately below the emergent layer, as is total plant cover (Figs. 7-9). The low vine cover in the emergent layer may

be a result of the inability of vines to find supports for climbing to the uppermost branches of emergent trees (Putz 1982). Light saturation within the canopy may also be a factor.

Finally, it should be noted that, to facilitate sampling, all populations were chosen from areas of intermediate vine density. Populations of widely-scattered individuals with low cover and those with very high density and essentially 100% cover also occur regularity (Warshauer et al. 1983). The former are found principally in the 'Ola'a Tract and the latter throughout most of the upper-elevation forests (1500-200 m) of the Hilo and Manowaialee Forest Reserves at Laupahoehoe.

CONCLUSIONS

Passiflora mollissima utilizes an an effective, diverse pattern of resource allocation ("strategy") which is principally adapted to pioneer situations but also embodies features of climax species. This introduced liana displays a wide ecological amplitude in all phases of its life cycle. Responses to environmental factors by this plastic species are characteristically variable.

The life cycle is characterized by a continuous, prolific seed rain and a fairly large, persistant bank of slow-growing shade-tolerant seedlings. Seed germination is staggered and seeds require a short period period of afterripening. Germination rates are extremely plastic but most seeds germinate within 6 months of ripening. Viability in fairly long for a tropical species (at least 1 year). Growth rates in the juvenile phase are rapid; under favorable conditions individuals reach reproductive maturity at an early age.

The breeding system of P. mollissima combines outcrossing with autogamy. Asexual reproduction (adventitious rooting) is present in low frequency, at the wetter sites. All phases of growth and reproduction are continuous and asynchronous within populations and on individuals. Peak flowering is in the dry, summer months; peak fruiting in the wet, winter months. Mortality is low after the establishment and the life span can exceed 20 years.

The combination of this diverse, opportunistic "strategy" with a general lack of predators and pathogens, favorable environmental conditions in Hawaiian forests (Chpt. 4) and effective dispersal by exotic mammals and birds has allowed P. mollissima to invade and maintain populations in a diverse array of habitats in Hawai'i. Functioning as a fast-growing heliophyte under open-canopy conditions, it also ocupies shaded habitats in the mature forests through "gap-phase" replacment.

CHAPTER FOUR

ESTABLISHMENT OF *PASSIFLORA MOLLISSIMA* IN THE CLOSED-CANOPY FORESTS OF HAWAI'I THROUGH THE MECHANISM OF GAP-PHASE REPLACEMENT

INTRODUCTION

The rapid growth of climbers is a characteristic feature of sunny, open sites and considered, by some authors, an expression of heliophily in these species (Richards 1952; Fogge 1960; Walter 1971). Liana thickets are a regular feature of areas where natural succession is held back by frequent disturbances (Webb 1958; Jones and Gray 1977; Crow 1980). These thickets represent a pioneer or seral stage; generally succession favors replacement of these heliophytes (Greig-Smith 1952; Dawkins 1961; Budowski 1965).

Several studies of native forest communities in Hawai'i have indicated that spread and dominance of *Passiflora mollissima*, an exotic vine, is aided by factors which disturb the overstory and understory vegetation (Jacobi and Warshauer 1975; Scowcroft and Nelson 1976; Burton 1980; Mueller-Dombois et al. 1981). *Passiflora mollissima* is a species of wide ecological amplitude, occurring in a variety of habitats in Hawai'i. Although present in both open and closed forests, the densest populations are found in open forests, often with histories of disturbance.

The 'Ola'a Tract section of Hawai'i Volcanoes National Park contains large areas of closed-canopy treefern (*Cibotium* spp.) forests with emergent 'ohi'a (*Metrosideros collina*). Introduced into the area in 1958 (Wong 1971), this exotic vine has spread rapidly: cover estimates show an 18-fold increase in 10 years (Warshauer et al. 1983). A severe windstorm in 1980, resulting in heavy disturbance to the emergent and treefern canopies, is considered the single most important factor responsible for the increase in *P. mollissima* cover in the 'Ola'a Tract. This increase and the patchwork pattern of distribution found in the 'Ola'a Tract suggest that this vine spreads by gap-phase invasion and regeneration, a common phenomenon in species found in the dense shade of tropical forest understories (Lebron 1979; Wallace and Dunn 1980).

METHODS

The Effect of Light on the Growth and Establishment of *Passiflora mollissima*

Artificially-controlled Shade

Seeds were collected from ripe fruit at Laupahoehoe and 'Ola'a at two week intervals, washed free of pulp and air dried for 24 hours before planting. Five seeds were planted in each of

10 pots filled with vermiculite mixed with the prescribed dosage of "Gaviota" time-release 14-14-14 fertilizer. Seedings were repeated twice at two week intervals. Pots were placed on a bench under clear fiberglass skylights and watered daily. The date of emergence was recorded for all seedlings.

Eight weeks after the emergence of the first seedlings, individuals were grouped according to their emergence date, into 2, 4 and 6-week old seedlings. Plants were segregated by age (2,4,6-week old) into two groups; one group (8 per age) was harvested, separated into root, stem and leaf components, dried at 80 ^{o}C for 48 hours, and weighed. Leaf area (cm^2) was measured, at the time of harvest, with a LI-COR LI 3050A optical planimeter. The height (cm) of all seedlings was also measured. In the other group, the height of all seedlings was measured and they were randomly assigned to one of five light intensity treatments with eight seedlings of each age per treatment (n=7 for 6-week old seedlings). Plants were placed under shade according to a split-plot design to avoid mutual shading.

Light intensities were regulated by varying amounts of nylon shade cloth and averaged 0.35%, 2%, 14%, 30% and 100% of full sun. Intensities were simultaneuously measured in the open (full sun: 100% RLI) and under each shade treatment with a pair of matched Weston Illumination meters equipped with a silicon photodiode which measures the incoming radiation in the 400 to 700 nm wavelenghths. Values in the full sun ranged from 1000 footcandles under heavy cloud cover to 10,000 foot candles under the brightest conditions (230-2300 uE/m^2 s). Emphasis was placed on lower light intensities in an attempt to more accurately determine the theoretical light compensation point (Harper 1977). Average ambient noon air temperatures under various light intensities were as follows: 100% RLI - 26.1 ^{o}C, 30% RLI - 22.4 ^{o}C, 14% RLI - 21.7 ^{o}C, 2% RLI - 20.7 ^{o}C and 0.35% RLI - 21.0 ^{o}C. Soil temperatures were measured at 2 cm below the surface, each day at noon, with a Tele-Thermometer (Precision Instruments) equipped with a soil probe. After 15 days, treated plants were harvested and treated as in the first group.

The partitioned dry weights were used to determine the relative biomass of each component (root, stem, leaf) under each light intensity. Relative growth rates and leaf areas were calculated using the following formulas (Cooper 1966; Radford 1967):

1. RELATIVE GROWTH RATE (WEIGHT) =
   (ln W2 - ln W1) / time

2. NET ASSIMILATION RATE (WEIGHT) =
   (((W2 - W1)/(lfar2 - lfar1))
   (ln lfar2 - ln lfar1) / tIme

3. LEAF AREA RATIO =
   ((lfar2 - lfar1) (ln W2 - ln W1)) /
   ((ln lfar2 - ln lfar1) (W2 - W1))

4. LEAF WEIGHT RATIO =
((lfwt2 - lfwt1) (ln W2 - ln W1)) /
((ln lfwt2 - ln lfwt1) (W2 - W1))

5. SPECIFIC LEAF AREA =
((lfar2 - lfar1) (ln lfwt2 - ln lfwt1)) /
((ln lfar2 - ln lfar1) (lfwt2 - lfwt1))

Where W1 = initial weight (mg)
W2 = final weight (mg)
lfwt1 = initial leaf weight (mg)
lfwt2 = final leaf weight (mg)
lfar1 = initial leaf area (cm^2)
lfar2 = final leaf area (cm^2)
totwt1 = initial total plant weight (mg)
totwt2 = final total plant weight (mg)
time = 15 days

Dimensional analysis (Barbour et al. 1980) was employed using data from the first harvest, to derive an empirical relationship between height and weight of seedlings at each age. These regressions were then used to estimate the weight of seedlings prior to treatment. An average value from the first harvest (for each age) was used as the initial weight and area of leaves.

Data from partitioned dry weights and growth measurements were subjected to an analysis of variance (SAS GLM Program) to determine if significant treatment effects existed. Duncan's Multiple Range Test was used to identify which light intensities and ages produced significantly different effects.

Natural Shade-Field Experiment

Twenty 10 by 10 m contiguous plots were marked out in a treefern (Cibotium) dominated forest with scattered emergent Metrosideros trees (Burton 1980; Burton and Mueller-Dombois in press). Twenty-five percent, 50%, 75%, 100% and 0% (control) of the treefern fronds were cut and removed from the plots, resulting in relative light intensities (RLI) of 15%, 17%, 27%, 43% and 10% (control) of full sun, respectively (Burton and Mueller-Dombois in press). Each treatment was replicated four times. The desired openness was maintained by periodic removal of Cibotium fiddleheads as they appeared. All herbaceous and undergrowth species were left undisturbed.

The final standing biomass (g dry wt.), density (no./200 m^2) and percent cover were selected as indices of Passiflora mollissima growth 12 to 14 months later. Final standing biomass and density were measured directly and percent cover was estimated by Burton (unpublished) using the Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974). All individuals of P. mollissima within the study plots were tallied

by plot, harvested, dried and weighed. Before drying, the plants were partitioned into stems, including tendrils, leaves and reproductive parts, (and roots in the case of germinants and seedlings) and assigned to one of four defined age classes as follows:

germinants--individuals without true leaves, only cotyledons present;
seedlings--non-reproductive individuals with true leaves but without tendrils;
juveniles--non-reproductive individuals with tendrils; and
adults--reproductive individuals.

Biomass of seedlings and germinants were combined in a single class (seedling) due to their relatively insignificant biomass.

For one year following the harvesting of P. mollissima, no Cibotium fronds were removed and the canopy within the plots was allowed to recover. At the end of the year, all plots were resurveyed for the presence of P. mollissima. The density of individuals (by age class) within each plot was recorded. Due to the small number of individuals present, no biomass measurements were made.

Data were averaged for each treatment and plotted against relative light intensity. Twenty-five percent and 50% canopy removal were combined into a single class, 16% RLI, due to the small difference in light intensity encountered under both treatments. No further quantitative analyses were performed on the data due to the uncontrolled nature of the study. Nevertheless, it provides a valuable insight into germination and growth, following canopy disturbance, under field conditions.

RESULTS

Light and Establishment

Artificial Shade

Prior to shading, all plants received near-maximal sunlight. As a result, effects of shading include any adjustments to various levels of shade made during the initial phase of the experiment.

Light intensity produced highly significant effects ($p=0.0001$) on the overall relative growth rate, and its components net assimilation rate and leaf area ratio (Table 13). The leaf area ratio (LAR) was generally inversely proportional to light intensity. At relative light intensities less than 14% however, differences in leaf area ratio were not statistically significant (Table 13). Transformation of the relative light intensity to a logarithmic scale emphasizes the differences in the rate of change (slope) of the LAR among light intensities (Fig. 25). It is evident that this rate is greater at higher light intensities and negligible at lower ones. This relationship is fairly consistent at different ages (Fig. 25).

The components of leaf area ratio, leaf weight ratio and specific leaf area, were significantly affected by light intensity but differed in their response to varying intensities (Table 13). The leaf weight ratio was lowest at 14% RLI and increased at higher and lower light intensities. In contrast, the specific leaf area was inversely proportional to light intensity but was unaffected by relative intensities less than 14% (Table 13). Although age had no significant effect on the overall mean leaf weight ratio ($p=0.5$), as age increased the difference in this ratio among light intensities was reduced (Table 14). The response curves for specific leaf area were similar for all was similar for all ages however, as age increased, the area was less affected by light of higher relative intensity (Table 14).

Net assimilation rates increased four-fold with increased light intensity, except for an anomalous decrease in 6-week old plants at 0.35% RLI (Table 14). The relationship between net assimilation rate and the logarithm of relative light intensity was curvilinear, over the wide range of light intensities, at all ages (Fig. 25). The sigmoid shape of the curve in 2 and 4-week old plants, indicates small changes in net assimilation rate at intermediate (2-14% RLI) light intensities and relatively large rates at higher and lower intensities. In 6-week old plants the slope was exponential, indicating greater increases in net assimilation rate at higher light intensities.

Relative growth rates increased with light intensity: maximum growth occurred at full sun (100% RLI) (Table 13). All ages responded similarly except for an unaccountable decrease in relative growth rate of 6-week old plants at 0.35 RLI (Table 14). Although age had no effect on the overall relative growth rate ($p=0.7$) younger plants grew considerably slower under low light intensities (Table 14) and "negative growth" occurred in some 2-week old plants. The sigmoid shape of the relative growth rate curves generally followed those of net assimilation rates, except for 2-week old plants, where the relationship was nearly linear (Fig. 25). The steep slope between 14% and 100% RLI indicates a rapid rise in the relative growth rate associated with a rise in net assimilation rate. The more gradual slope of the relative growth rate, compared with that of net assimilation rate, was due to the contribution of changes in the leaf area ratio to the overall relative growth rate. The gradual slope of the relative growth rate between 14% and 2% RLI is indicative of a slight decrease in the rate of growth with increased shade at this light level.

Age significantly affected the mean net assimilation rate and leaf area ratio ($p=0.0001$) but had no effect on the relative growth rate ($p=0.7$), at this stage of development. Net assimilation rates were highest in 6-week old plants but this increase was offset by a lower leaf area ratio, resulting in no net gain in mean relative growth rate (Table 14). The lower leaf area ratio in older individuals was a result of they smaller

specific leaf area in 6-week old plants (Table 14); the leaf weight ratio was unaffected by age ($p=0.5$).

Height growth increased with plant age (Fig. 25) although this measurement was not adjusted for initial plant size, as was the relative growth rate based on weight changes. Growth in height was proportional to light intensity up to 14% RLI in 2-week old plants and 30% RLI in 4 and 6-week old plants then declined with increased light. An unaccountable decrease in height (growth) occurred between 0.35% RLI and 2.0% RLI in 6-week old seedlings.

Natural Shade-Field Experiment

No individuals of P. mollissima were found in the study plots at the time of initial frond removal except for 1 juvenile with low cover (0.1%; Burton; unpublished data), in a 75% removal plot (27% RLI) After fourteen months of canopy removal, the average density of Passiflora mollissima increased up to 5 fold with increased light intensity (Fig. 27). The highest average density, 5.4 indiv. per 200 m^2, occurred at 27% relative light intensity (RLI). Densities were equivalent in control plots (10% RLI) and under 100% canopy removal (43% RLI). Juveniles occurred in the highest density, adults were few in number (Fig. 27). Biomass increased 300-fold with increased light intensity from an average of 0.5 g per 200 m^2 in control plots (10% RLI: 0% canopy removal) to 145 g per 200 m^2 in 100% removal plots (43% RLI) (Fig. 28). In contrast to density, the biomass of adults exceeded that of all other age groups, while germinants and seedlings accumulated little biomass (Fig. 28).

Highest densities of germinants were in control plots; seedlings in 27% RLI plots (Fig. 27). No germinants or seedlings occurred in 43% RLI plots (100% removal) at the time of harvest. The biomass of germinants and seedlings increased slightly with light intensity up to 27% RLI (Fig. 28). Juvenile biomass increased from 0.9 g per 200 m^2 in control plots (10% RLI) to 132 g per 200 m^2 in 100% removal plots (43% RLI). All increases in biomass were accompanied by higher densities, except at 43% RLI.

Adults occurred in very low density in 27% and 43% RLI plots and were absent at lower light intensities (Fig. 27). The presence of a single individual in 27% RLI plots resulted in a substantial increase in biomass between 16% and 27% RLI (Fig. 23).

When plots were resurveyed one year after the harvest of P. mollissima (1981), only ten new individuals were collected from the 20 study plots. This represents a 200-fold decrease in density from the time of initial P. mollissima harvest (1980) (Table 15). No individuals were found in control plots in 1981; the remaining treatments averaged less than one individual per 200 m^2. Of the ten individuals present in 1981, eight were juveniles, one was a seedling and the remaining one was a

reproductive individual approximately four meters tall. The latter individual occurred in a 100% canopy removal plot (43% RLI).

DISCUSSION

The relative growth rate of a plant is dependent upon the efficiency of the assimilatory system (net assimilation rate; NAR) and the proportion of photosynthetic area to plant weight (leaf area ratio; LAR). This relationship can be expressed mathematically as the product of these two functions (NAR, LAR: Blackman and Wilson 1951). Plant growth rate potentials are determined by genetically fixed internal factors but subject to modification by environmental factors, such as light and temperature (Grime 1966). They may also vary with the stage of plant development (Blackman and Wilson 1951; Grime 1966; Yamaguchi and Friend 1979).

Light intensity affects the growth and morphology of Passiflora mollissima. Changes in the relative growth rate (and its components NAR and LAR) largely determine the shade tolerance of this plant and its competitive ability in closed canopy forests of Hawai'i. In the early stages of development, P. mollissima functions as a facultative sciophyte, combining characteristics of shade tolerant and intolerant plants. Unlike obligate sciophytes (shade plants), which characteristically reach optimum photosynthesis and growth at intermediate light intensities (10-20% RLI; Bannister 1976), the growth rate of P. mollissima increases rapidly at higher light intensities. Optimal growth occurs in full sunlight (Fig. 25). The overall growth rates of P. mollissima are comparable to those reported for the fast-growing annual Helianthus (Blackman and Wilson 1951; Blackman and Black 1959).

Rapid growth of P. mollissima at high light intensities is associated with a greater net assimilation rate. Although rates increase with plant age (and size), these increases are offset by reductions in the relative size of the assimilatory system (LAR) (Table 14). Consequently, age has no effect on mean relative growth rates during the early stages of development. This is evident by the difference in slope between the rates of net assimilation and relative growth (Fig. 25): as age increases, so does the difference between the net assimilation and relative growth rates. In 6 week old plants, the former increases exponentially; corresponding increases in the latter are linear.

Greatest shade tolerance is exhibited at intermediate to low light intensities (14%-2% RLI), where relative growth rates decrease slightly with increased shade. Greater tolerance is a consequence of an increasingly efficient asimilatory system (small decrease in NAR) and a concurrent increase in the photosynthetic area (LAR), with increasing shade (Fig. 25). The significant increase in leaf area ratio at intermediate light

intensities is due to greater leaf expansion (specific leaf area), a common phenomenon in shade tolerant plants exposed to low light intensities (Grime 1965).

Very low light intensities severely restrict growth and may prevent establishment at this stage of development. When the relative light intensity is less than 2%, no further leaf expansion occurs and the leaf area ratio remains fairly constant while net assimilation rates decline rapidly. Consequently, under these conditions, plants show a sharp decrease in relative growth and therefore, a lower degree of shade tolerance (Fig. 25) (Blackman and Black 1959). The higher relative growth rate in 6 week old plants, under conditions of 0.35% RLI, appears anomalous in light of other results.

Inhibition of growth by dense shade decreases with age in the early stages of development. Growth rates were reduced 93% from full sun to dense shade (0.35% RLI) in 2 week old plants, 70% in 4 week old plants and only 46% in 6 week old plants (Table 14). Experimental results indicate that the growth response is plastic and some younger individuals (2 weeks old) are below the compensation point at very low light intensities (less than 0.35% RLI). The intolerance of P. mollissima to deep shade is supported by the abscence of individuals from densely-shaded exotic tree plantations such as tropical ash (Fraxinus uhdei (Wenzig) Lingelsh.) and sugi pine (Cryptomeria japonica (L. f.) D. Don), while surrounding areas of more open native forest support dense populations of the vine.

Before leaving the subject of relative growth rates, the effect of temperature should be noted. Temperatures varied 6 °C from full sun to the deepest shade (0.35% RLI) and some of the increase in growth rates at higher light intensities may be attributed to temperature effects. In any case, the effects of these factors (light and temperature) are very closely-related in nature.

The competetive ability of a plant is directly related to its leaf area index and increase in dry matter (biomass), but in the early stages of development in low light environments, it may depend equally upon the relative growth in height among species. Although many plants can tolerate deep shade, such conditions are suboptimal and growth is generally favored by the higher light intensities at greater heights. In addition, the suppression of root growth at low light intensities may have negative effects on seedling survival when moisture is limiting (Cooper 1967). At intermediate to low light intensities plants become etiolated and growth in height is rapid (Fig. 26). At lower light intensities, this elongation is accompanied by a suppression of leaf growth but at slightly higher intensities, leaf area also increases (Table 14). At relative light intensities greater than 30%, height growth is suppressed, although biomass (weight) continues to increase (Fig. 26).

The patchwork pattern of P. mollissima distribution in 'Ola'a and its response to experimental canopy removal indicate that successful establishment and regeneration of populations is dependent upon regular disturbances to the canopy and that the size and nature of these gaps determines the nature of the ensuing population. The phenomenon of "gap-phase" replacement is common in species growing in the dense shade of tropical forests, where light is a limiting factor (Lebron 1979; Wallace & Dunn 1980).

Gap formation is a regular feature of Cibotium forests. Small gaps in the tree-fern canopy are associated with the collapse of dead or senescent trees and windthrows of shallow-rooted emergents. Direct damage to the Cibotium fronds results from moderate-intensity windstorms which occur irregularly. The tree-fern canopy may also be disturbed locally due to the activities of feral pigs. Large scale disturbance of the Cibotium canopy occurs following heavy windstorms, such as the January 1980 storm, which occur on the average once every three to four years (Blumenstock 1967). Following such a storm, in January of 1980, a perceptible increase in the cover and abundance of P. mollissima was evident within a few months.

The establishment of P. mollissima in the closed Cibotium forest of 'Ola'a is associated with its shade tolerance in the seedling stage and its capacity for rapid height growth under suitable conditions. In the abscence of gap-formation, populations may be maintained by low numbers of shade tolerant seedlings, exemplified by the presence of widely scattered seedlings in remote, relatively undisturbed portions of the 'Ola'a Tract.

Seed germination in P. mollissima is stimulated by the increased light intensity and temperatures associated with canopy disturbance (Chapter 3). The rapid and fairly synchronous colonization of plots following canopy removal (Fig. 29) and the abscence of germinants and seedlings in 100% removal plots 14 months later indicate that colonization was due largely to the germination of dormant seeds present in plots at the time of disturbance rather than an influx of seeds via dispersal. This conclusion is supported by the low number of individuals reappearing in plots one year after cessation of canopy disturbance and removal of P. mollissima (Table 15). The extended viability (up to 18 months) and presence of a dormancy mechanism in seeds of P. mollissima have been demonstrated (Chapter 3). Elsewhere in the tropics, similar conditions of increased light and temperature were found to stimulate germination of dormant seeds of "gap-phase" and secondary forest species (Meijer 1970; Quarterman 1970; Lebron 1979).

The magnitude of the disturbance, or gap size, and resulting differences in light intensity and related factors clearly affect the rate and pattern of establishment (Fig. 30). Accepting seedling establishment as the point at which they have "expanded

a photosynthetic surface and are capable of independent existence" (Harper 1977) and the insignificant contribution by germinants and seedlings to total biomass (Fig. 28), negligible increases in biomass and cover would be expected prior to establishment. Following this period, significant increases in cover (and therefore biomass) may be attributed to a growth phase.

Cover was inappreciable in control plots (10% relative light intensity) after 14 months of canopy disturbance indicating little establishment. Analysis of the final population structure and biomass confirmed that few germinants became established and little biomass accumulated. With increased light intensity, establishment was accelerated and a growth phase, accompanied by substantial increases in biomass, occurred (Fig. 30). The positive effects of light on growth of P. mollissima have also been demonstrated under experimental conditions (Table 14). At higher relative light intensities the increase in cover exhibited a tendency towards equilibrium, however there was insufficient data available to distinguish among: 1. a true equilibrium condition, 2. a temporary reduction in growth due to adverse environmental conditions such as the summer dry period or 3. intra or inter-specific competition effects.

The depletion of the seed bank following initial disturbance suggests that future colonizations may be largely dependent upon seed dispersal into the area. However, seeds are regularly and effectively disseminated by feral pigs and birds.

Results of both controlled and field experiments have indicated that within small gaps, light may limit the success of P. mollissima; growth rates may be insufficient for individuals to reach the canopy before gap closure occurs. Following canopy closure, growth and reproduction are largely restricted to the canopy. Few leaves are supported in the shade of the understory and death of apices is common. This reduced vigor suggests that shade tolerance may be lost with increasing age. In larger openings, growth exceeds a critical level and individuals rapidly reach the canopy, before gap closure, and reproduce. According to Burton's (1980) estimates of frond (Cibotium) regrowth, P. mollissima may become firmly established in the canopy, following disturbance, well before the one to five years necessary for canopy closure. The presence of a reproductive individual in the 100% removal plots, one year after cessation of disturbance and removal of all P. mollissima, confirms that some time is needed for the mitigation of the effects of more extensive canopy disturbance. Following this stage, individuals are no longer inhibited by the increased shade formed with canopy closure, and frequently spread laterally through the canopy.

Further support for the hypothesis of gap-phase invasion and regeneration by P. mollissima comes from population structure analysis at two sites within the interior of 'Ola'a with histories of disturbance (Fig. 5). At site 'Ola'a-2, disturbance

has been in the form of occasional, small gaps in the canopy. The wide range of vine diameters present and density of reproduction classes indicates an established, reproducing population. The somewhat irregular distribution of density within the diameter classes, (the discontinuous distribution and higher density in the largest size class), suggests that small, periodic perturbations, resulting in recurrent bursts of growth and establishment, may have occurred.

The situation at site 'Ola'a-1 is very different. Much of the canopy is dead or dying as a result of 'ohi'a decline (Mueller-Dombois et al. 1980) and the canopy is quite open. The tree fern subcanopy is only poorly developed and numerous exotic heliophytes are present. The presence of a single large individual in a distribution otherwise skewed to low diameters indicates that initial colonization occurred some time ago but the population was slow to establish. This hypothesis is supported by evidence from aerial photographs. Photos of the area prior to the introduction of P. mollissima, and shortly thereafter (1954, 1965), show little canopy dieback while more recent photos (1979) indicate extensive canopy dieback. The high cover values and adequate reproduction currently found at this site suggest that the population is now firmly established (Figs. 5,9).

The competitive position of P. mollissima in 'Ola'a is aided by conditions associated with canopy disturbance. Comparison of the growth rates of P. mollissima with those of Metrosideros suggests that following a disturbance, P. mollissima would outcompete regenerating Metrosideros , which are also dependent upon canopy disturbance in closed-canopy forests (Burton and Mueller-Dombois in press). Under field conditions, seedling growth and establishment of Metrosideros was adversely affected by higher light intensities and associated conditions (higher temperatures and lowered relative humidity). In contrast, optimal growth of P. mollissima occurs in full sun (under controlled conditions) and field observations indicate that seedlings are moderately drought tolerant.

CONCLUSIONS

Growth and establishment of P. mollissima is proportional to light intensity and associated factors, such as higher temperatures. Although closed-canopy forests are not optimal habitats, they are susceptible to invasion and infestation by this exotic vine, with regular disturbances to the canopy, through the mechanism of "gap-phase" replacement. Effective dispersal of seeds by feral pigs and birds provides a bank of widely-scattered seedlings which are fairly shade-tolerant and capable of exploiting canopy gaps, as they occur. This combination of effective dispersal and "gap-phase" regeneration are largely responsibe for the patchwork pattern of distribution in the 'Ola'a Tract and the rapid increase in cover obsered within the last ten years.

ACKNOWLEDGEMENTS

No thesis is ever the sole work of the author. Rather it represents the composite efforts and ideas of a wide range of people. This work is no exception. I would like to thank my fellow graduate students and the faculty of the Botany Department for their ideas and support in the course of this work. In particular I would like to acknowledge my committee members, both interim and final: Drs. Gerald Carr, Charles Lamoureux, Dieter Mueller-Dombois, Clifford Smith and Sanford Siegel. The assistance and cooperation of several agencies greatly facilitated my field research, data analysis and preparation of this manuscript. They include the staffs of the Research Management Division of Hawaii Volcanoes National Park, Hawaii Division of Forestry, Institute of Pacific Island Forestry, Fish and Wildlife Service (Volcano), State Parks and the Kokee Museum. I would also like to thank Drs. Gerald Carr, Douglas Friend, Charles Lamoureux, Sanford Siegel and Francis Putz for reviewing various portions of this manuscript, Dr. Kim Bridges and June Saito for their technical assistance on the computer and Dina Kageler and George Linney for their photography.

Drs. Linda Escobar and Larry Gilbert provided much-needed unpublished information on Passiflora mollissima in its native habitat and Dr. Escobar identified specimens of Passiflora mollissima. Phil Burton provided me with unpublished data on the growth of banana poka. The cooperation of these people is greatly appreciated. A very special aloha goes to several people for their support "above and beyond the call". Dina Kageler and Daniel Lepine put in many long thankless hours in the field, helping to collect data during the summers of 1980-81. Christa Russell and Bob Cessaro graciously provided me with a home and much moral support in the "final days". Finally my sincere thanks go to Dr. Clifford Smith whose support and guidance throughout this study have made it a reality.

Funding for this study was made available through a grant from the Cooperative National Parks Resource Studies Unit (University of Hawai'i; Department of Botany: NPS contract CA 8001 2 0001), Dr. C. W. Smith, Unit Director and a grant from the Institute of Pacific Islands Forestry (U.S.D.A) (P.O 40 9231 1 126). Supplemental funding was also supplied by Dr. Mueller-Dombois, Hawaii Division of Forestry and Pacific Tropical Botanical Gardens.

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Table 1. *Comparison of some descriptive characters of the Hawaiian representatives of* Passiflora mollisima (HBK.) Bailey with South American forms of P. mollissima and P. mixta L.

character	locality	mean		range	
		Passiflora mollissima	Passiflora mixta	Passiflora mollissima	Passiflora mixta
leaf blades (l)	Hawai'i	12.1		6.1 - 18.7	
	South America	8.3	6.5	5.3 - 17.0	3.5 - 12.0
leaf blades (w)	Hawai'i	17.8		8.1 - 29.5	
	South America	10.0	9.5	7.0 - 25.0	5.0 - 18.5
petiole (l)	Hawai'i	3.3		1.2 - 6.7	
	South America	2.2	2.0	1.5 - 3.0	0.9 - 8.0
petiolar glands (no)	Hawai'i	6		4 - 9	
	South America	-	-	6 - 14	4 - 10
peduncle (l)	Hawai'i	3.6		1.5 - 6.6	
	South America	4.3	3.1	1.8 - 10.5	1.0 - 9.0
bract (l)	Hawai'i	4.2		3.3 - 4.9	
	South America	3.4	4.2	2.5 - 5.7	1.2 - 7.5
hypanthium (l)	Hawai'i	7.0		4.7 - 8.0	
	South America	8.9	9.5	5.5 - 11.8	7.0 - 14.0
hypanthium (d)	Hawai'i	1.0		0.8 - 1.2	
	South America	1.2	1.1	-	0.5 - 1.5
sepal (l)	Hawai'i	5.1		3.8 - 5.9	
	South America	3.4	4.0	2.4 - 5.5	2.3 - 5.5
sepal (w)	Hawai'i	1.9		1.4 - 2.5	
	South America	1.0	1.4	-	0.9 - 2.1
fruit (l)	Hawai'i	9.9		7.3 - 13.2	
	South America	-	-	6.0 - 11.0	4.0 - 7.2
fruit (w)	Hawai'i	3.4		2.4 - 4.1	
	South America	-	-	3.0 - 4.5	2.0 - 3.5
seed (l)	Hawai'i	5.9		5.0 - 7.0	
	South America	6.0	-	-	3.5 - 5.0
seed (w)	Hawai'i	4.2		4.0 - 5.0	
	South America	4.5	-	-	2.0 - 4.0

All measurements in cm except seeds in mm.

Hawaiian populations of P. mollissima average and range of 100 individuals sampled in 1981.

South American populations of P. molissima and P. mixta average and range as reported by Escobar (1980).

(l) = length, (w) = width, (d) = diameter, (no) = number.

Table 2. Summary of the physical features of the seven population structural analysis sites on the island of Hawai'i. Rainfall and temperature data from the nearest meteorological station (State of Hawai'i 1970). Vegetation classifications from draft vegetation maps compiled by J. D. Jacobi as a part of the U. S. Fish and Wildlife Service's Hawai'i Forest Bird Survey. Soil information from Sato et al. 1973 (soil maps).

site	elevation (m)	climate type	mean annual rainfall (mm)	mean annual temperature (°C)	vegetation classification	soil subgroup
Kaloko-1	1410	seasonal forest winter-dry	997	15.9	c3Me,2nt(W:ns-tf-xs)	typic tropofolists
Kaloko-2	1443	seasonal forest winter-dry	997	15.9	c3Me,2nt(M:ns-xg)	hydric, lithic dystrandepts
Laupahoehoe-1	1780	seasonal forest summer-dry	2151	11.7	c3Ac-Me,2nt(M:ns-Pm)	hydric dystrandepts
Laupahoehoe-2	1250	seasonal forest summer-dry	2151	14.5	c3Ac-Me,2nt(W:tf,ns)	typic hydrandepts
Laupahoehoe-3	1580	seasonal forest summer-dry	2151	12.5	o3Ac-Me,2nt(M:ns-Pm,xg)	typic hydrandepts
'Ola'a-1	1188	rainforest	2880	13.9	c3Me,2nt(W:tf,ns)sng	lithic tropofolists
'Ola'a-2	1130	rainforest	2880	13.9	s3Me,2nt(W:tf,ns)	typic hydrandepts

Legend for vegetation classification is as follows: i.e. site Kaloko-1 $\frac{1}{c}\ \frac{2}{3\ Me,2nt}\ \frac{3}{(W:ns\text{-}tf\text{-}xs)}\ \frac{4}{}\ \frac{5}{}$.

1. tree canopy cover: c=closed (>60% cover); o=open (25-60%); s=scattered (<25%). 2. tree canopy height: 3=>10 m tall; 2=5-10 m tall and tree species composition: Ac=Acacia koa; Me=Metrosideros collina; nt=native tree association. 3. general habitat type: W=wet; M=mesic. 4. understory species composition; ns=native shrub; tf=tree fern; xs=exotic shrub; xg=exotic grass; Pm=Passiflora mollissima. 5. other information: sng=many standing dead or defoliated trees. Dash indicates species codominance.

Table 3. Effect of light intensity on the germination of Passiflora mollissima under two diurnal temperature regimes at Volcano, Hawai'i. Duncan's Multiple Range Test: means in the same row with the same letter are not significantly different; values a-c ranked in descending order. (P = 0.05.)

		relative light intensity				
germination	station	--- / 0.35%	3.6% / 2.0%	10.0% / 14.0%	33.0% / 30.0%	100.0%† / 100.0%‡
success (%)	V1	---	58.6^{a} ±18.3	65.3^{a} ± 5.0	77.7^{a} ± 7.7	16.7^{b} ± 7.7
success (%)	V2	40.0^{a} ±12.0	46.4^{a} ±14.8	41.2^{a} ±11.2	34.4^{a} ± 4.8	45.2^{a} ±16.8
ND_{50}	V1	---	60.0^{a} ± 4.6	52.0^{a} ± 0.7	50.0^{a} ± 2.0	49.6^{a} ± 4.2
ND_{50}	V2	63.0^{c} ± 3.2	47.3^{b} ± 0.3	45.0^{ab} ± 0.6	42.0^{ab} ± 0.6	40.3^{a} ± 0.3

† relative light intensities at station Volcano-1

‡ relative light intensities at station Volcano-2

ND_{50} = number of days to one-half maximum germination

Table 4. Effect of dry storage and pig ingestion on the germination of Passiflora mollissima. Duncan's Multiple Range Test: means in the same row with the same letter are not significantly different; values a-b ranked in descending order. (P = 0.05.) Average of four replicates; n=50 for each replicate.

variable	seed treatment			
	fresh	dry storage	captive pig	feral pig (field scats)
dry weight of seeds (mg)	287.9^{a} ±4.9	---	289.6^{a} ± 3.7	250.5^{b} ±5.4
germination success (%)	63.2^{a} ±9.8	75.2^{a} ±6.6	32.0^{b} ± 6.4	78.0^{a} ±9.6
ND_{50} germination	80.3^{b} ±6.8	25.7^{a} ±0.2	70.3^{b} ±20.1	31.0^{a} ±0.6

ND_{50} = number of days to one-half maximum germination

Table 5. Density (number/hectare) and survival (percent) of Passiflora mollissima at seven selected sites on the island of Hawai'i. Sites: K = Kaloko; L = Laupahoehoe; O = 'Ola'a.

	density				survival	
site	germinant (<0.1 m)	establishment (0.1 - 1.0 m)	established (>1.0 m)	total	germinant to establishment	establishment to established
K1	3640	4610	1116	9410	127%	24%
K2	121600	3700	1590	126890	3%	43%
L1	4707	393	387	5487	8%	98%
L2	554000	1700	775	556475	0.3%	46%
L3	267879	750	458	269078	0.3%	61%
O1	638	625	500	1763	97%	80%
O2	2957	1200	700	4857	40%	58%

Table 6. The growth rate of Passiflora mollissima at three stages in the life history.

growth characteristic	age	growth rates	
		mean	range
daily increase in shoot length (cm)	seedling	0.07 ±0.004	0 - 0.22
	juvenile	0.25 ±0.017	0 - 0.84
	adult	0.19 ±0.015	0 - 0.71
daily increase in mean internode length (cm)	seedling	0.0033 ±0.0002	0 - 0.011
	juvenile	0.0092 ±0.0007	0 - 0.033
	adult	0.0076 ±0.0006	0 - 0.30
yearly increase in diameter (mm)	juvenile	1.52 ±0.1	0 - 5.0
	adult	1.41 ±0.01	0 - 4.9

Table 7. The effects of site and age on the growth of Passiflora mollissima. Duncan's Multiple Range Test: means (site) in the same row with the same letter are not significantly different, means (age) in the same column with the same number are not significantly different, means listed in descending order. (P = 0.05.)

growth characteristic	age	site		
		Kaloko	Laupahoehoe	'Ola'a
daily increase in shoot length (cm)	seedling	0.040^{b-2}	0.079^{a-3}	0.092^{a-2}
	juvenile	0.122^{c-1}	0.277^{b-1}	0.361^{a-1}
	adult	0.161^{a-1}	0.169^{a-2}	0.233^{a-2}
daily increase in mean internode length (cm)	seedling	0.0014^{b-2}	0.0047^{a-2}	0.0040^{a-3}
	juvenile	0.0044^{b-1}	0.0106^{a-1}	0.0129^{a-1}
	adult	0.0051^{b-1}	0.0094^{a-1}	0.0084^{a-2}
yearly increase in shoot diameter (mm)	juvenile	2.56^{a-2}	2.34^{b-2}	1.88^{c-2}
	adult	3.00^{a-1}	2.76^{b-1}	2.78^{b-1}

Table 8. Seasonal index of shoot growth in length (cm/day) and diameter (mm/yr) of *Passiflora mollissima* at three stages in the life cycle, based on the sine-function $Y = a + b \cdot \sin((c+X) \cdot 2\ d^{-1})$ (Bridges et al. 1981); a = monthly mean; b = overall amplitude; c = displacement or maximum value; r = Pearson's correlation coefficient.

age	growth	r	mean	amplitude	date of maximum
seedling	length	0.57	0.067	0.021	Jul 6
juvenile	length	0.30	0.024	0.031	Jun 21
	diameter	0.12	1.8	0.086	Feb 15
adult	length	0.77	0.16	0.085	Aug 16
	diameter	0.26	1.7	0.26	Jul 6

Table 9. Results of pollination experiments conducted on Passiflora mollissima from January to March 1982 at 'Ola'a, Hawai'i. N = 50; x and y represent the number of tagged peduncles located after three and ten weeks, respectively.

treatment	breeding system	x	% fruit set at three weeks	y	% fruit set at ten weeks
flowers emasculated, bagged; not pollinated	apogamy	49	0	---	---
stigmas removed; flowers bagged	apogamy	44	0	---	---
flowers bagged (natural selfing)	autogamy	49	6.52	48	4.17
flowers bagged; hand-pollinated (forced selfing)	autogamy	49	65.31	41	51.22
flowers not bagged (open pollination)	autogamy or exogamy	49	40.82	46	15.22

Table 10. Stepwise regressions of temperature, daylength and rainfall, with 0, 1, 2 and 3 month lags, on the seasonality of flushing, anthesis and fruiting of Passiflora mollissima in Hawai'i. Data are used for three sites on Hawai'i and three sites in South America which support populations of the vine. Only the variable which best explains the observed variation in phenological activity is listed.

		phenophase		
site	latitude	flush	anthesis	fruit
Hawai'i (all sites)	20 N	- mntemp3 r^2=0.217 ***	- mxtemp3 r^2=0.097 ***	- mntemp0 r^2=0.462 ***
Kaloko		+ rain1 r^2=0.457 **	+ mntemp0 r^2=0.318 *	+ mntemp0 r^2=0.567 **
Laupahoehoe		- mntemp3 r^2=0.372 **	- mxtemp0 r^2=0.380 **	- mntemp r^2=0.543 **
'Ola'a		- mntemp3 r^2=0.321 *	+ rain0 r^2=0.130 **	- rain1 r^2=0.194
Bogota Colombia	5 N	day3 r^2=0.410 **	+ rain0 r^2=0.116	---
Quito Ecuador	0	- rain2 r^2=0.071	- rain3 r^2=0.079	- temp0 r^2=0.099
Huancayo Peru	10 S	day3 r^2=0.994 ***	day3 r^2=0.414 **	- temp1 r^2=0.102

+, - indicate slope of regression

* significant at P=0.05 ** significant at P=0.01 *** significant at P=0.001

Table 11. Comparison of the general features of the climates of Passiflora mollissima habitats in South America (native) and Hawai'i (introduced).

	area	
climatic variable	Hawai'i	South America
annual daylength difference	02:24	00:02 to 01:11
average annual temperature (°C)	11 - 18	6 - 20
annual variation in temperature (°C)	2 - 3	3 - 6
average annual rainfall (mm)	1000 - 2900	750 - 2000
dry season	Jun - Sep	Jun - Aug
wet season	Nov - Mar	Nov - Mar
temperatures in dry season	decreasing	increasing
fog	frequent heavy	frequent heavy

Table 12. Seasonality of the climates at three sites on the island of Hawai'i and in South America, based on the sine function $Y = a + b \cdot \sin((x + c) \cdot (6.28/12))$ (Bridges et al. 1981); r = Pearson's correlation coefficient; a = the mean value; b = the amplitude; c = the theoretical maximum (date).

climatic variable	region	site	r	a	b	c
daylength (hrs:min)	Hawai'i	all	0.990	12.04	1.12	May 18
	S. America	Bogota	0.937	12.07	0.13	Jun 12
	S. America	Quito	0.217	12.07	0.01	Nov 24
	S. America	Huancayo	0.990	12.07	0.35	Dec 3
temperature (°C)	Hawai'i	all	0.990	13.9	1.28	Aug 6
	S. America	Bogota	0.721	13.9	0.37	Mar 27
	S. America	Quito	0.136	13.2	0.02	Mar 15
	S. America	Huancayo	0.871	11.6	1.13	Dec 12
rainfall (mm)	Hawai'i	'Ola'a	0.878	237.1	124.8	Feb 15
	Hawai'i	Laupahoehoe	0.735	159.6	66.8	Jan 1
	Hawai'i	Kaloko	0.736	84.0	20.7	Apr 27
	S. America	Bogota	0.268	76.2	12.3	Nov 18
	S. America	Quito	0.778	105.9	52.9	Jan 30
	S. America	Huancayo	0.540	50.5	36.9	Dec 21

Table 13. The effect of light intensity on the relative growth rate and associated growth assessments of Passiflora mollissima. Values represent mean of 2, 4 and 6 week-old plants. Duncan's Multiple Range Test: means in the same row with the same letter are not significantly different; means (a-d) listed in descending order. Full sun = 100; range of noon light intensities in full sun: 230-2300 $\mu E \cdot m^{-2} \cdot s^{-1}$.

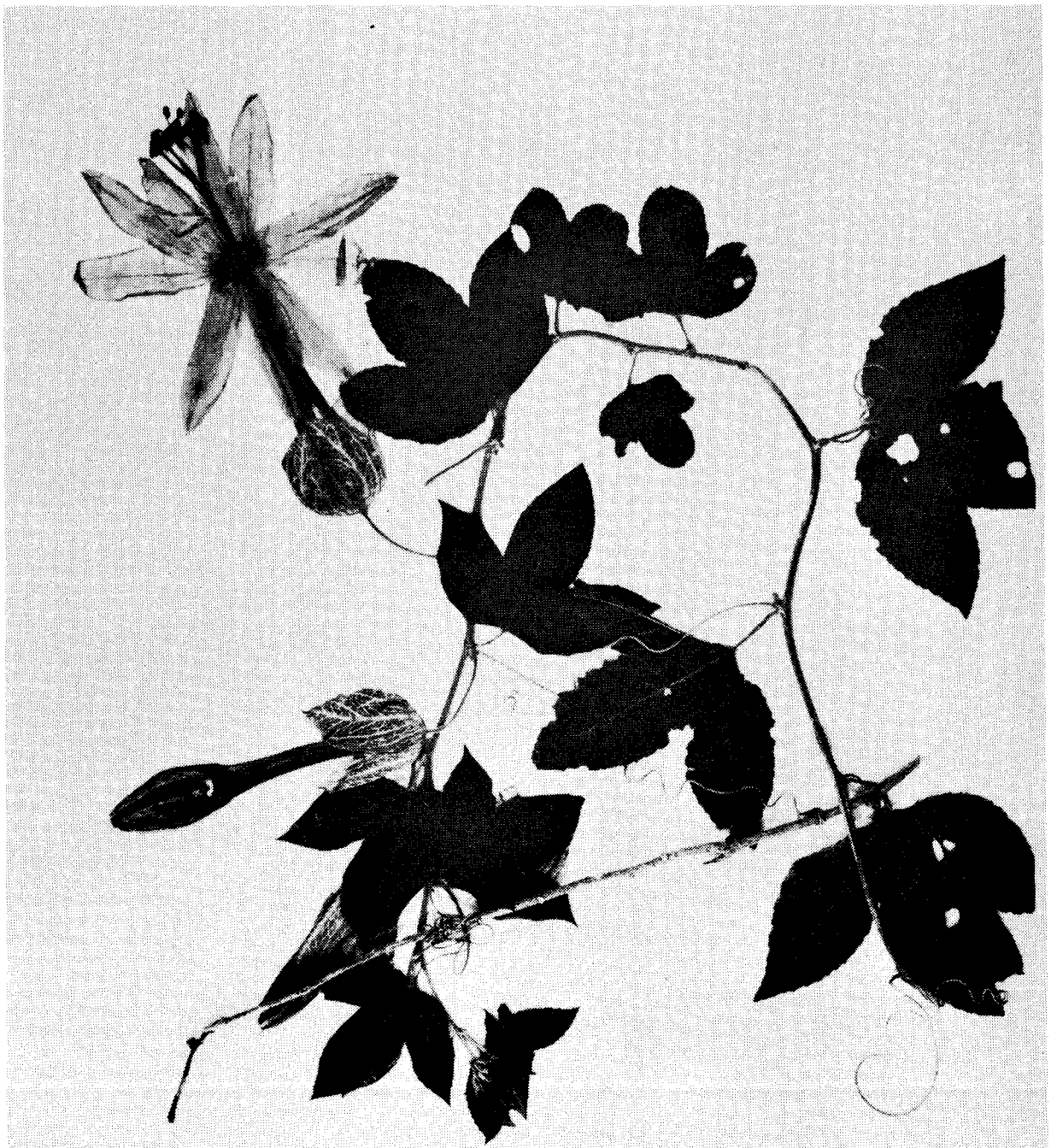
	relative light intensity				
variable	0.35	2.0	14.0	30.0	100.0
relative growth rate ($g/g \cdot day$)	0.035 ^{d}	0.054 ^{c}	0.077 ^{b}	0.094 ^{b}	0.122 ^{a}
net assimilation rate ($g/dm^{-2} \cdot day$)	0.0135 ^{d}	0.0185 ^{d}	0.0266 ^{c}	0.0384 ^{b}	0.0608 ^{a}
leaf area ratio (dm^{2}/g)	2.67 ^{a}	2.56 ^{a}	2.54 ^{a}	2.16 ^{b}	1.76 ^{c}
leaf weight ratio (g/g)	0.593 ^{a}	0.425 ^{bc}	0.378 ^{c}	0.418 ^{bc}	0.494 ^{ab}
specific leaf area (dm^{2}/g)	4.83 ^{a}	4.81 ^{a}	4.75 ^{a}	4.23 ^{b}	3.17 ^{c}

Table 14. The effect of light intensity on the relative growth rate, and its derivatives, of Passiflora mollissima at three stages of development. Duncan's Multiple Range Test: means in the same column with the same letter are not significantly different; means (a-d) listed in descending order. Full sun = 100; range of noon light intensities in full sun: 230-2300 $\mu E/m^2 \cdot s^1$.

variable	relative light intensity	initial age (weeks)		
		2	4	6
relative growth rate ($g/g \cdot day$)	0.35	0.009^{c}	0.034^{c}	0.063^{c}
	2.0	0.044^{c}	0.066^{b}	0.053^{c}
	14.0	0.082^{b}	0.074^{b}	0.074^{bc}
	30.0	0.103^{a}	0.087^{b}	0.091^{b}
	100.0	0.132^{a}	0.116^{a}	0.117^{a}
net assimilation rate ($g/dm^2 \cdot day$)	0.35	0.0038^{d}	0.0100^{d}	0.0253^{cd}
	2.0	0.0114^{cd}	0.0207^{c}	0.0225^{d}
	14.0	0.0203^{c}	0.0260^{b}	0.0338^{bc}
	30.0	0.0351^{b}	0.0365^{b}	0.0430^{a}
	100.0	0.0542^{a}	0.0609^{a}	0.0669^{a}
leaf area ratio (dm^2/g)	0.35	3.12^{a}	2.57^{a}	2.07^{a}
	2.0	3.36^{a}	2.37^{b}	2.27^{a}
	14.0	3.37^{a}	2.30^{b}	1.95^{ab}
	30.0	2.61^{b}	2.11^{b}	1.77^{ab}
	100.0	2.10^{c}	1.67^{c}	1.48^{b}
leaf weight ratio ($g \cdot g^{-1}$)	0.35	0.774^{a}	0.557^{a}	0.468^{b}
	2.0	0.337^{b}	0.445^{a}	0.493^{b}
	14.0	0.288^{b}	0.400^{bc}	0.456^{b}
	30.0	0.359^{b}	0.439^{bc}	0.456^{b}
	100.0	0.434^{b}	0.526^{b}	0.525^{a}
specific leaf area ($dm^2 \cdot g^{-1}$)	0.35	5.37^{a}	4.76^{a}	4.37^{a}
	2.0	5.46^{a}	4.42^{a}	4.55^{a}
	14.0	5.67^{a}	4.28^{a}	4.56^{a}
	30.0	4.59^{b}	4.22^{a}	3.87^{a}
	100.0	3.67^{c}	2.97^{b}	2.82^{b}

Table 15. Number of plants appearing in experimental plots at initial harvest, after one year of canopy disturbance (1980), and one year after initial harvest, following cessation of canopy disturbance (1981).

	stage of development				
year	germinant	seedling	juvenile	adult	total
1980	48	54	120	2	224
1981	0	1	8	1	10



Herbarium of the University of Hawaii

PLANTS OF THE HAWAIIAN ISLANDS

HAWAII

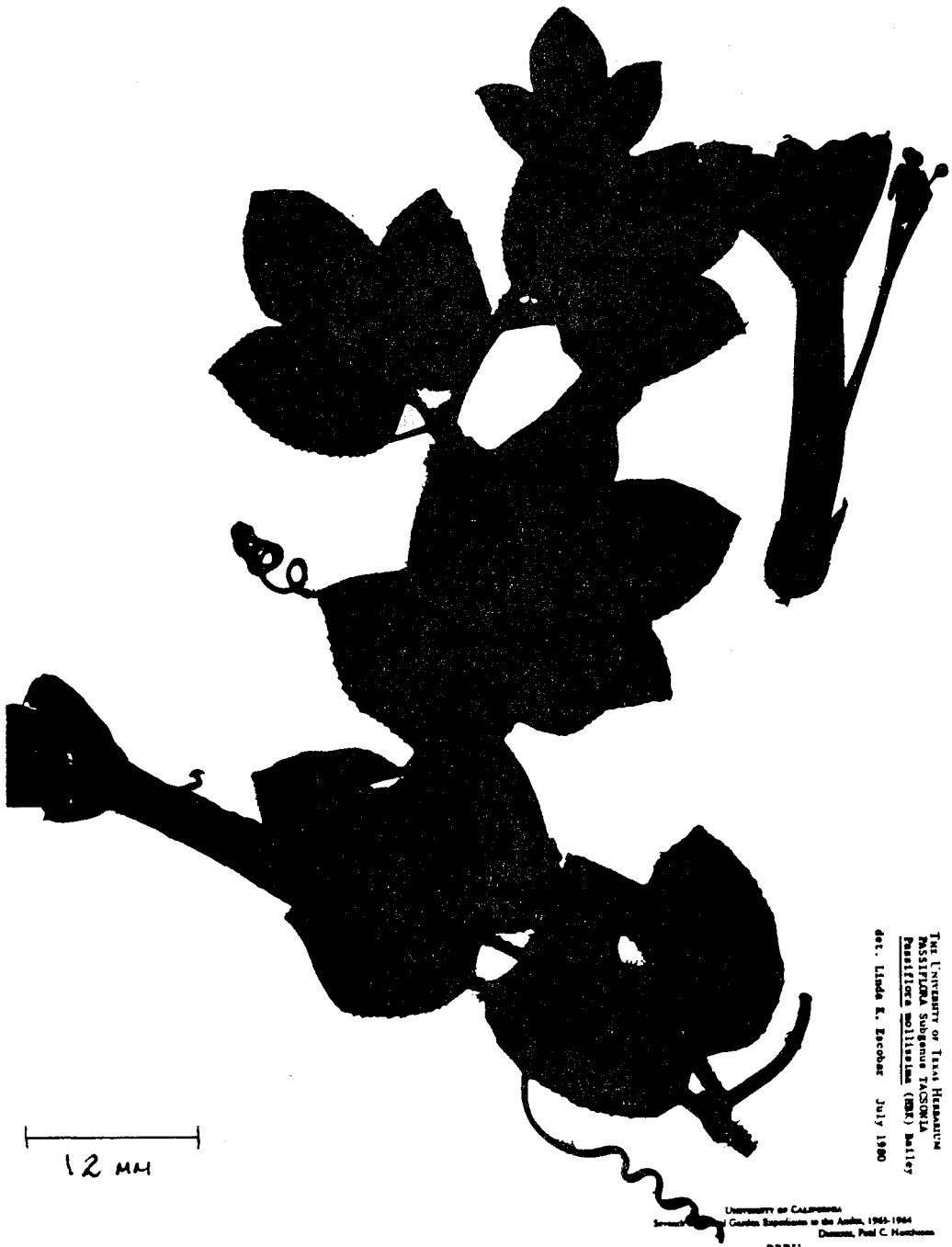
Passiflora mollissima(HBK)Bailey

Hawaii Volcanoes National Park
Ola'a Tract; behind Ag. Expt. Sta.
wet 'Ohi'a-Cibotium forest
Vine festooning trees, invading from road, reproduction abundant
Flowers pink; fruit yellow,downy
common name "Banana Poka"
EXOTIC elev. 1300 m

Coll. Anne Marie LaRosa

No. 7 Date 23 Feb. 1980

Fig. 2. Representative specimen of the typical form of Passiflora mollissima (HBK.) Bailey from South America. Note the general size and shape of flowers and leaves.



THE UNIVERSITY OF TEXAS HERBARIUM
PASSIFLORA Subgenus TACSONIA
Passiflora mollissima (HBK) Bailey
det. Linda K. Escobar July 1980

UNIVERSITY OF CALIFORNIA
Seventh Botanical Garden Expedition to the Andes, 1965-1966
Director, Paul C. Hutchison

PERU

Passiflora mollissima (HBK) Bail.
dupl. det. J. J. Wurdack, 1966

Road to Palmito.
Hacienda Tasin, between the Casa Hacienda and Palmito
Alt. 2500 - 3000 m
Province of Huaigayoc, Department of Cajamarca
PAUL C. HUTCHISON 6380
ELIAS VON BREMACK 31 August 1964
DISTRIBUTED BY THE HERBARIUM OF THE UNIVERSITY OF CALIFORNIA

Collection number 6380 . Sheet of sets 7 . Set 1, UC, determiner's nos. DB Duplicates UBBA, UC, F, NY, MO, K,

UNIVERSITY OF CALIFORNIA
Seventh Botanical Garden Expedition to the Andes, 1965-1966
Director, Paul C. Hutchison

Additional field notes for 6380 : Open hill in deciduous (or dying) trees. Flowers dark pink; rim of mouth with white spots rising from purple ring, the mouth below white. Filaments white, styles white, stigmas green, ovary green.

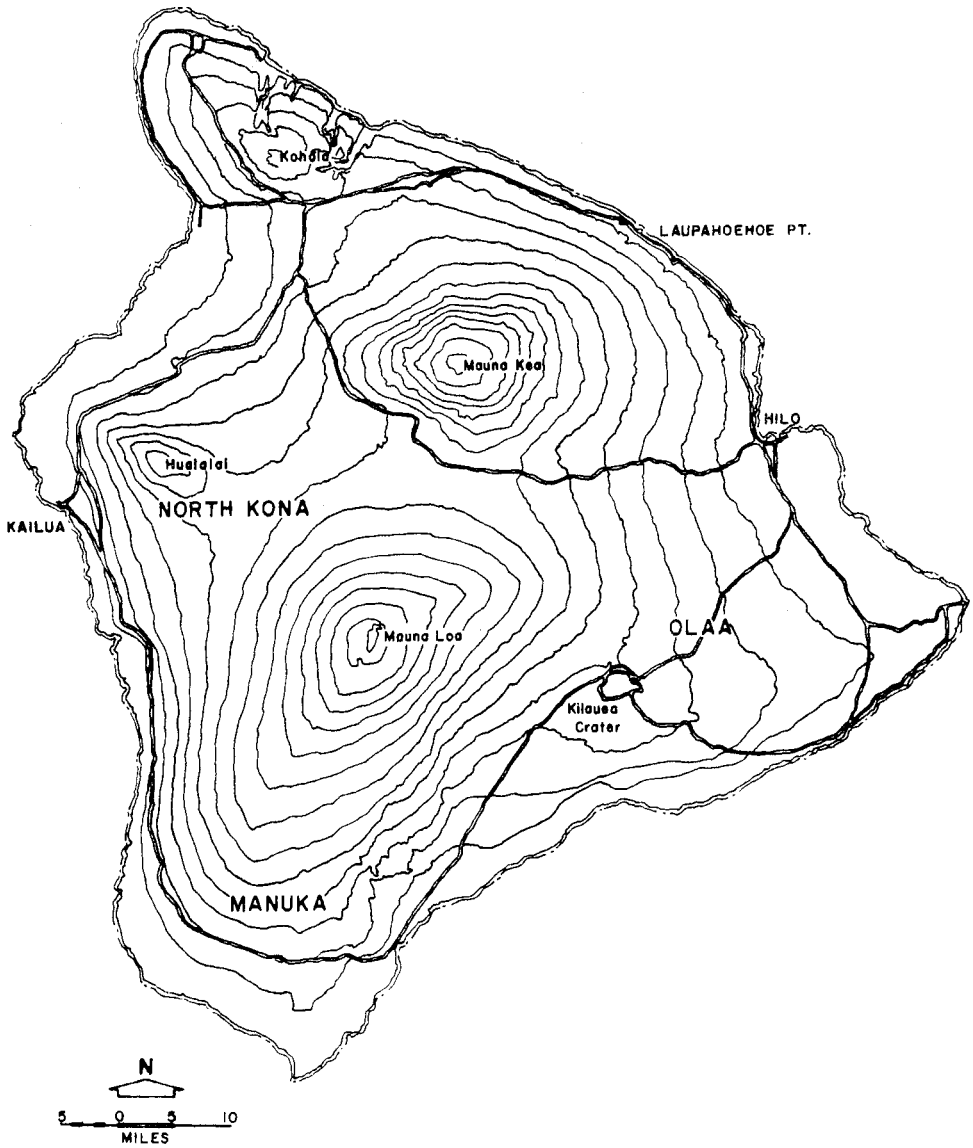
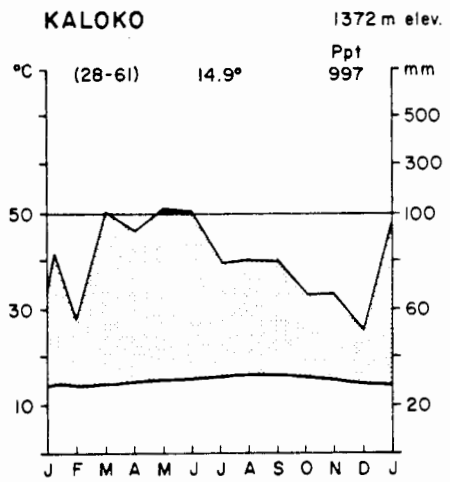
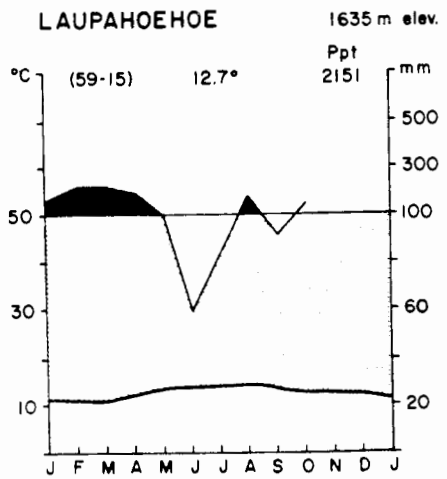
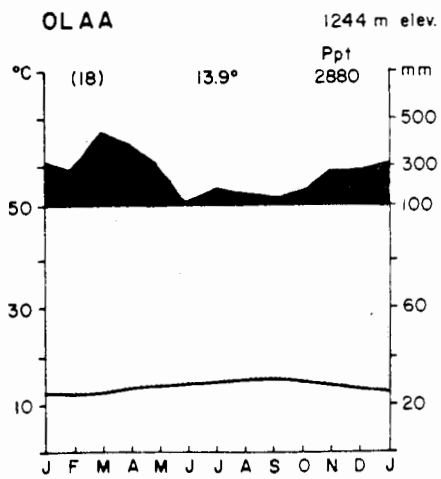


Fig. 3. Location of the three Passiflora mollissima study areas, Kaloko, Laupahoehoe and 'Ola'a, on the island of Hawai'i.

Fig. 4. Climate diagrams of the three study areas on the island of Hawai'i. Format follows Walter et al. (1975). The uppermost line represents mean monthly precipitation plotted with reference to the right-hand ordinate. The bottom line represents mean monthly air temperature plotted with reference to the left-hand ordinate. The mean annual precipitation is found in the upper right-hand corner of each diagram; the mean annual air temperature in the center. The figure in the upper left represents the number of years of observations for temperature and rainfall (respectively), or both, if only one number appears. Rainfall and temperature data are from the nearest meteorological station; long-term averages from State of Hawai'i (1970). Monthly rainfall values greater than 100 mm are indicated by blackened areas. Dotted areas represent "humid" periods.


KALOKO
1372 m elev.
Ppt
997
°C
(28-61)
14.9°
mm
500
300
50
100
30
60
10
20
J F M A M J J A S O N D J


LAUPAHOEHOE
1635 m elev.
Ppt
2151
°C
(59-15)
12.7°
mm
500
300
50
100
30
60
10
20
J F M A M J J A S O N D J


OLAA
1244 m elev.
Ppt
2880
°C
(18)
13.9°
mm
500
300
50
100
30
60
10
20
J F M A M J J A S O N D J

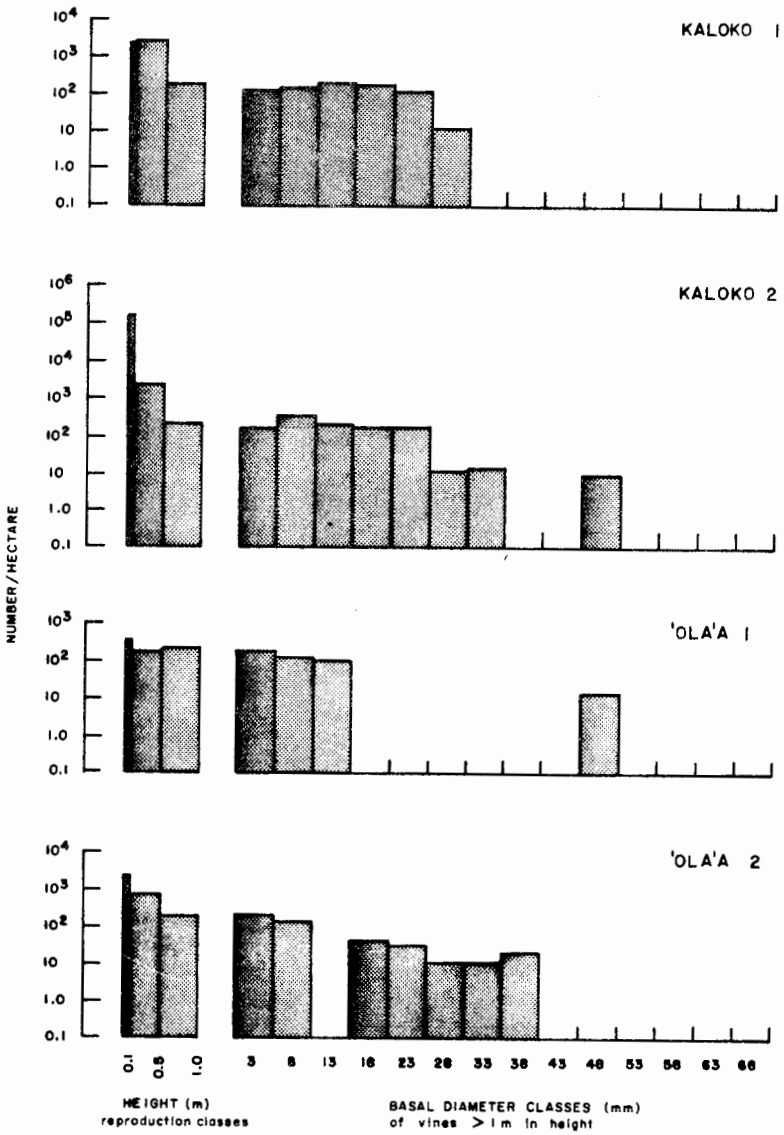


Fig. 5. Distribution of diameter and height classes of Passiflora mollissima at two sites in the Kaloko and 'Ola'a areas on the island of Hawai'i.

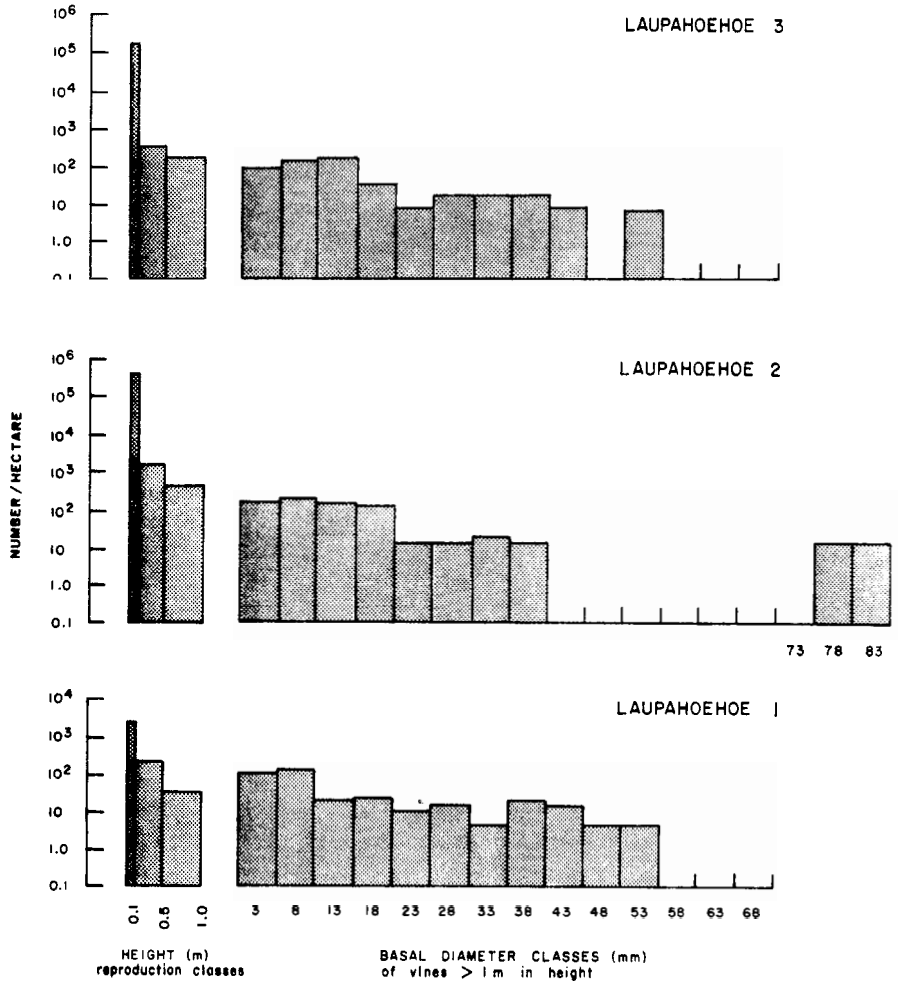


Fig. 6. Distribution of diameter and height classes of Passiflora mollissima at three sites in the Laupahoehoe area on the island of Hawai'i.

Fig. 7. The distribution of Passiflora mollissima density and cover and total plant cover in various vegetation layers at each site in the Kaloko area on the island of Hawai'i.

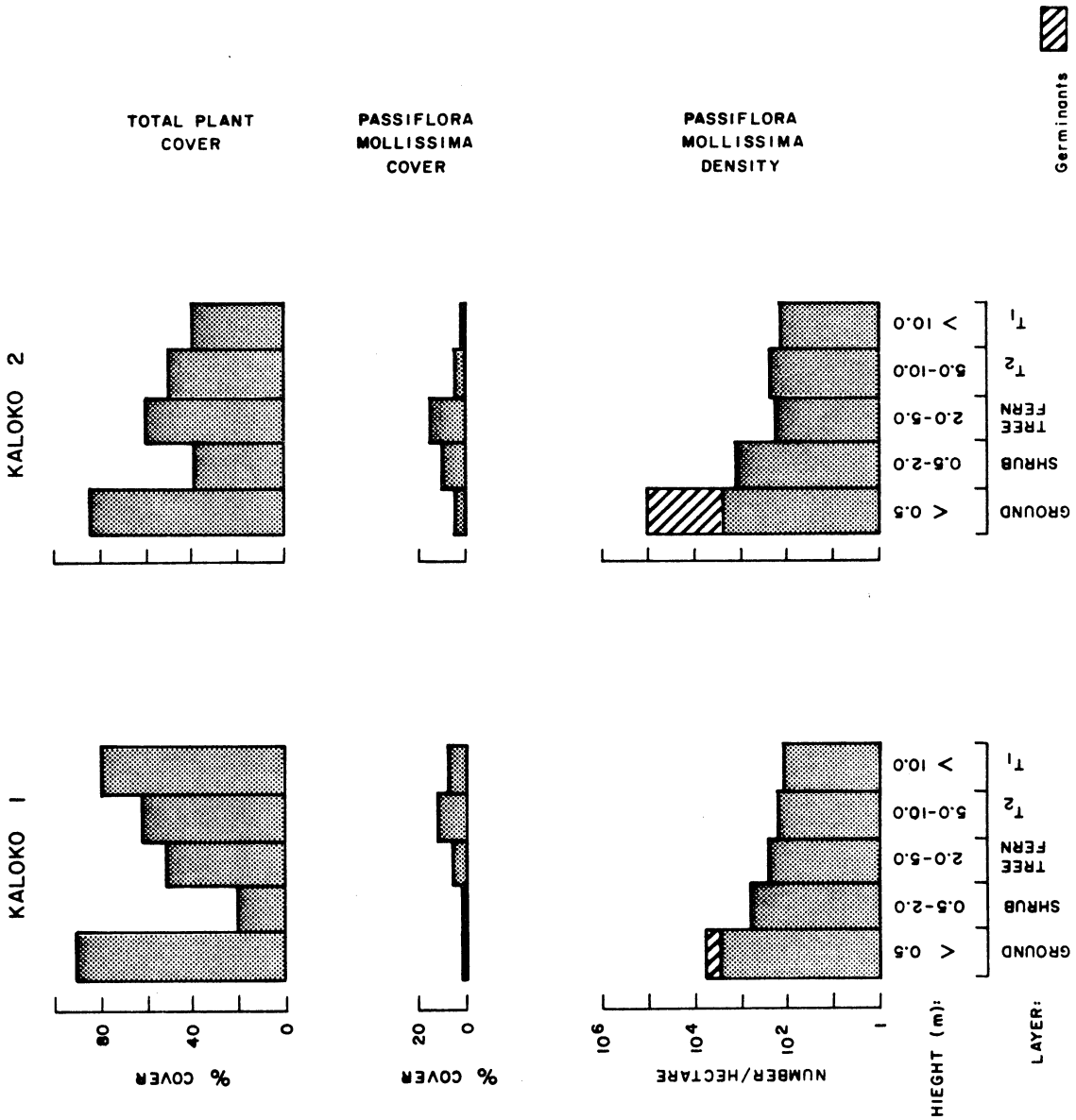

TOTAL PLANT COVER
PASSIFLORA MOLLISSIMA COVER
PASSIFLORA MOLLISSIMA DENSITY
Germinants
KALOKO 2
KALOKO 1
% COVER
80
40
0
20
0
NUMBER/HECTARE
10^6
10^4
10^2
1
HIEGHT (m):
LAYER:
GROUND
< 0.5
SHRUB
0.5-2.0
TREE FERN
2.0-5.0
T_2
5.0-10.0
T_1
> 10.0

Fig. 8. The distribution of Passiflora mollissima density and cover and total plant cover in various vegetation layers at each site in the Laupahoehoe area on the island of Hawai'i.

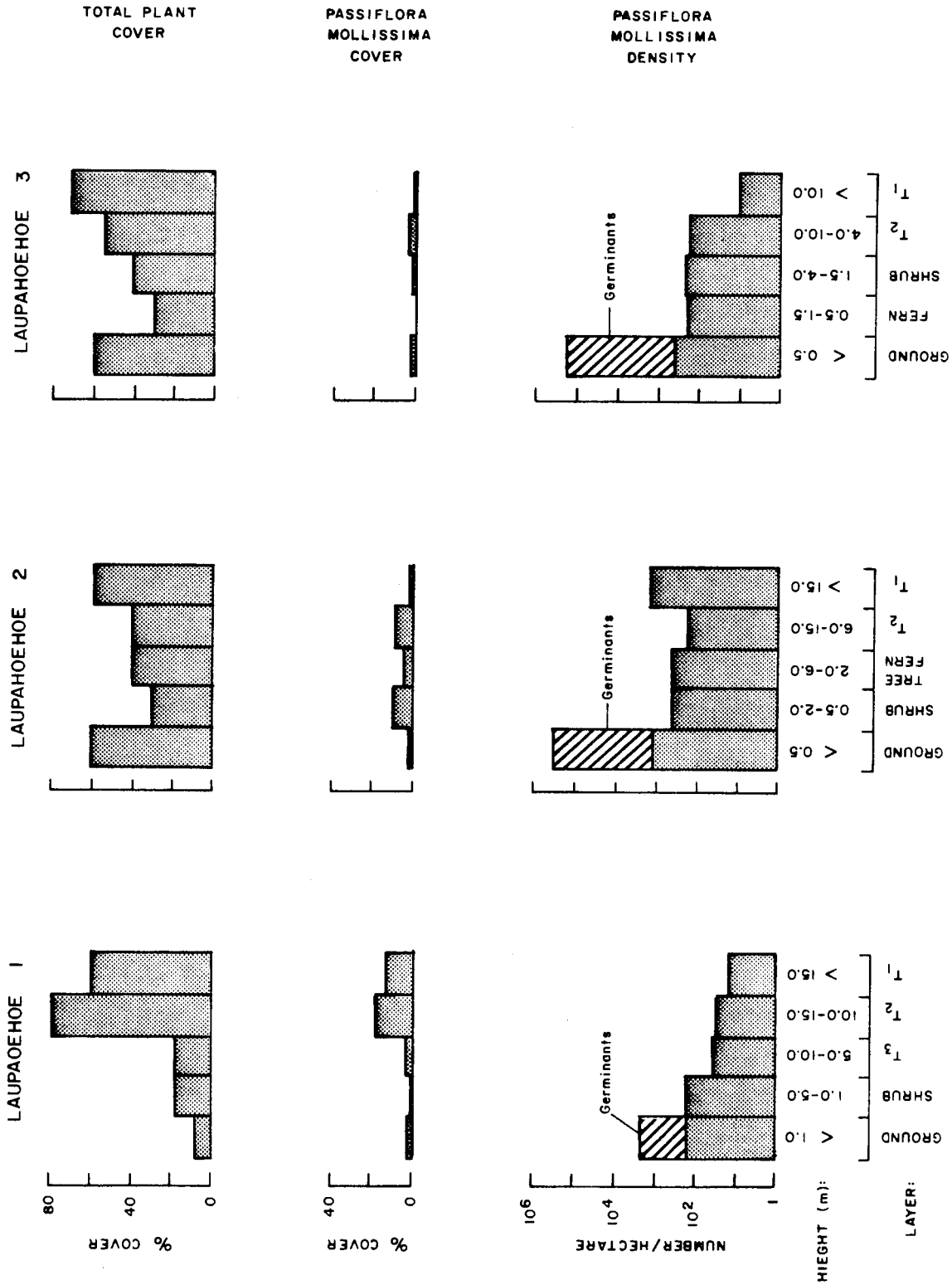
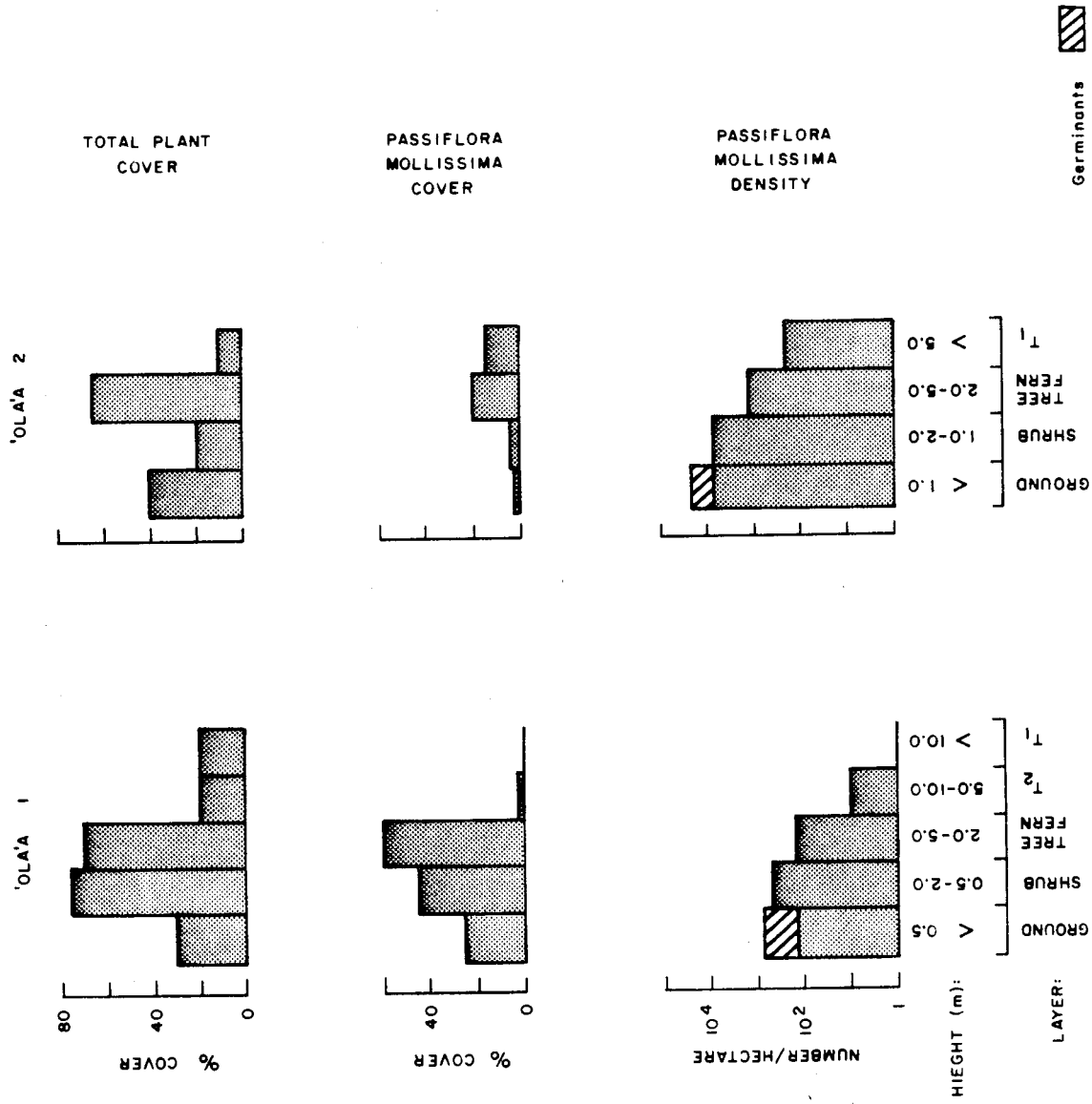

TOTAL PLANT COVER
PASSIFLORA MOLLISSIMA COVER
PASSIFLORA MOLLISSIMA DENSITY
LAUPAHOEHOE 3
LAUPAHOEHOE 2
LAUPAOEHOE 1
% COVER
80
40
0
40
0
NUMBER/HECTARE
10^6
10^4
10^2
1
Germinants
HIEGHT (m):
LAYER:
GROUND
< 0.5
FERN
0.5-1.5
SHRUB
1.5-4.0
T_2
4.0-10.0
T_1
> 10.0
GROUND
< 1.0
SHRUB
1.0-5.0
T_3
5.0-10.0
T_2
10.0-15.0
T_1
> 15.0
GROUND
< 0.5
SHRUB
0.5-2.0
TREE FERN
2.0-6.0
T_2
6.0-15.0
T_1
> 15.0

Fig. 9. The distribution of Passiflora mollissima density and cover and total plant cover in various vegetation layers at each site in the 'Ola'a Tract on the island of Hawai'i.


TOTAL PLANT COVER
PASSIFLORA MOLLISSIMA COVER
PASSIFLORA MOLLISSIMA DENSITY
Germinants
'OLA'A 2
'OLA'A 1
80
40
0
% COVER
40
0
% COVER
10^4
10^2
1
NUMBER/HECTARE
HIEGHT (m):
LAYER:
GROUND
SHRUB
TREE FERN
T_2
T_1
< 0.5
0.5-2.0
2.0-5.0
5.0-10.0
> 10.0
GROUND
SHRUB
TREE FERN
T_1
< 1.0
1.0-2.0
2.0-5.0
> 5.0

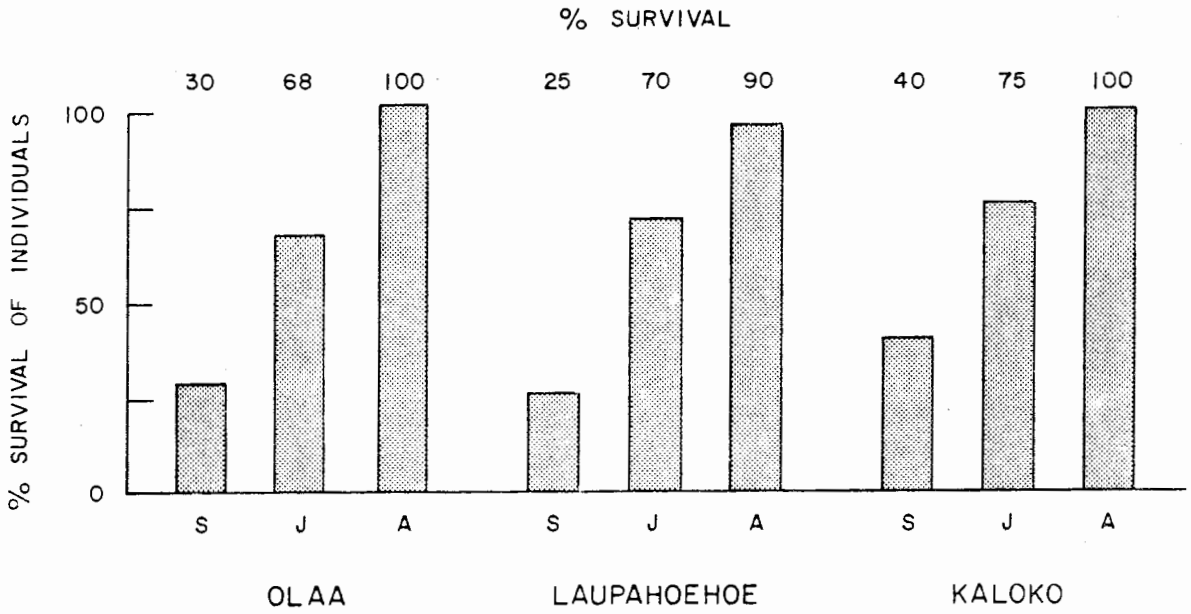


Fig. 10. Survival of seedlings, juveniles and adults of Passiflora mollissima, over an eighteen month period, at three sites on the island of Hawai'i.

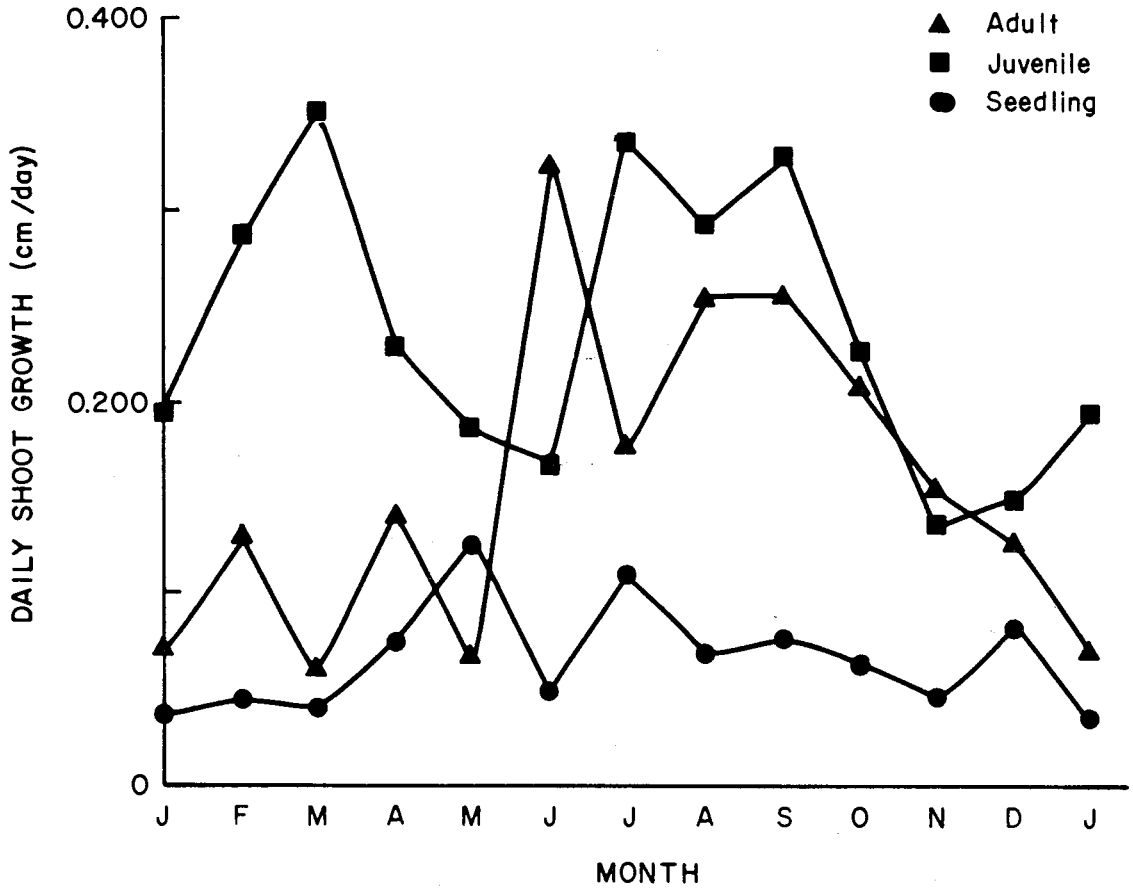
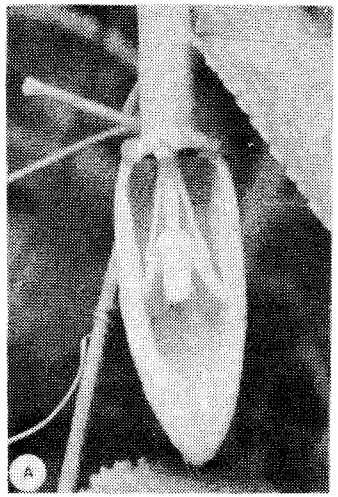
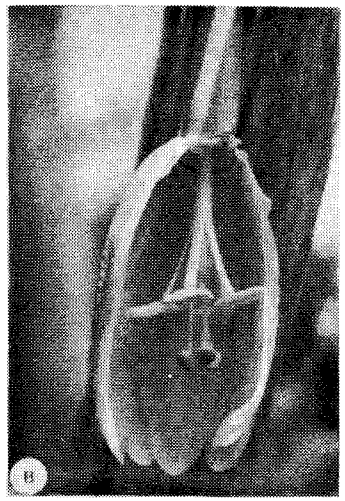


Fig. 11. Seasonal distribution of the daily shoot growth, as measured by changes in shoot length (cm/month), of Passiflora mollissima at three stages in the life cycle.

Fig. 12. Movement and position of various floral parts during anthesis in Passiflora mollissima. A. Flower prior to anthesis showing the appressed, introrse anthers. B. Flower at early anthesis (day 1). Anthers are oriented 90° from their original position (A). Note also the downward orientation of the stigmas and their position below the anthers. C. Close-up of the anthers and stigmas on day 1 of anthesis. Anthers are extrorse and styles have begun to curve upward and outward. D. Flower with perianth in horizontal position (day 1 or 2). Anthers are extrorse. E. Flower in its fully-reflexed position (late in day 1 or 2). F. Flower on day 3 of anthesis showing relaxed perianth and reproductive parts.


A


B


C


D


E

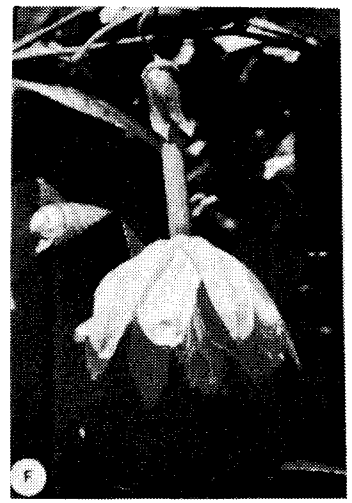
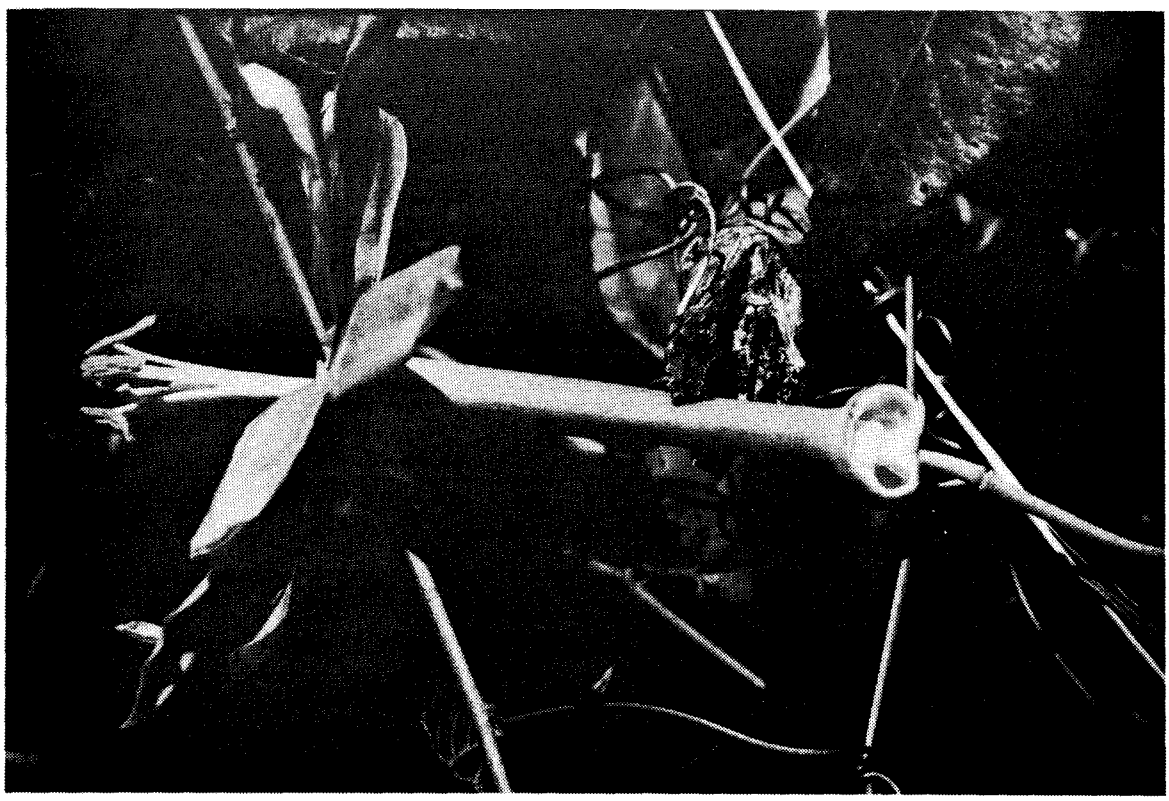

F

Fig. 13. Examples of herbivory on the nectar tube of flowers of Passiflora mollissima. Upper photo shows damage done by small herbivores, such as honey bees. Bottom photo illustrates damage from birds.



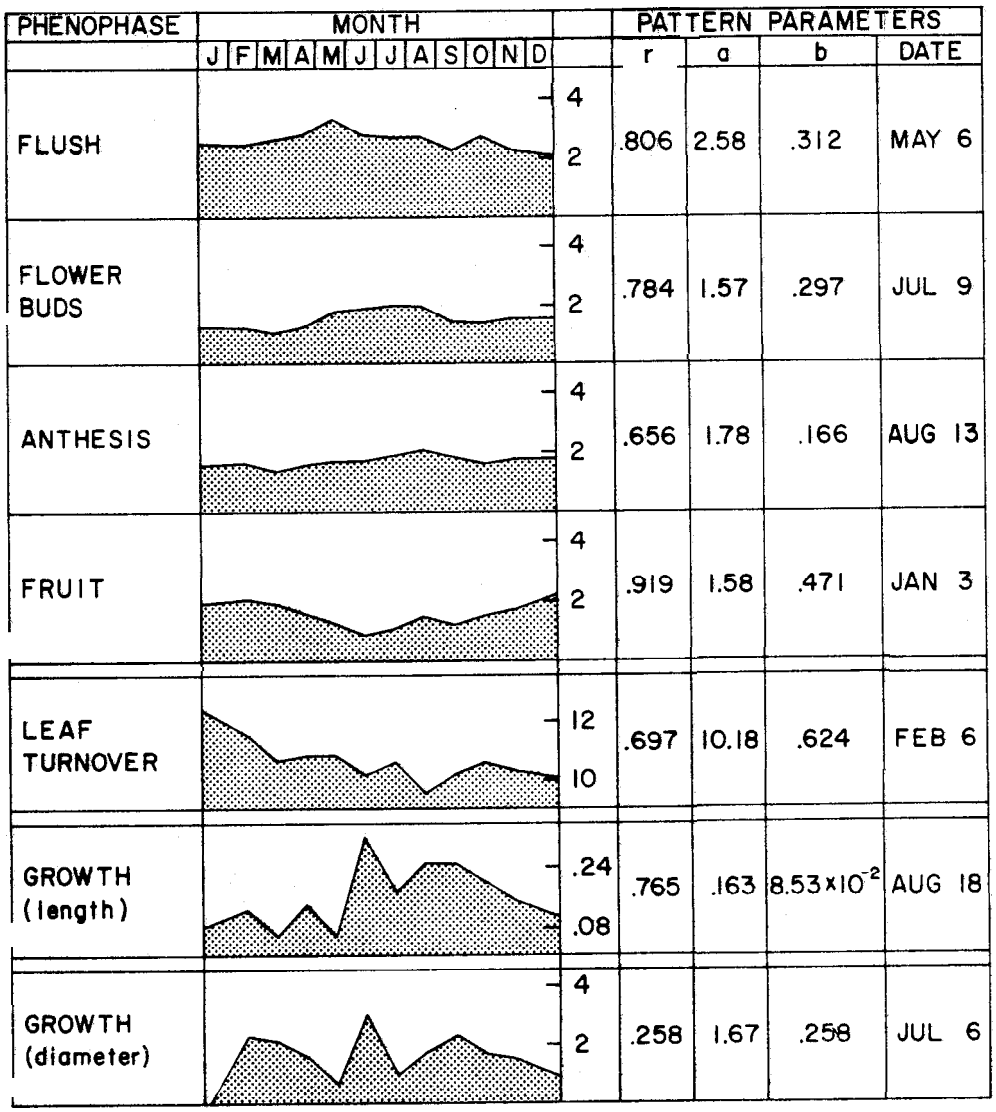


Fig. 14. The seasonal behavior of Passiflora mollissima in Hawai'i. Changes in the magnitude of the monthly growth and reproductive indices based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient. a = monthly mean. b = annual amplitude. c = displacement or maximum value.

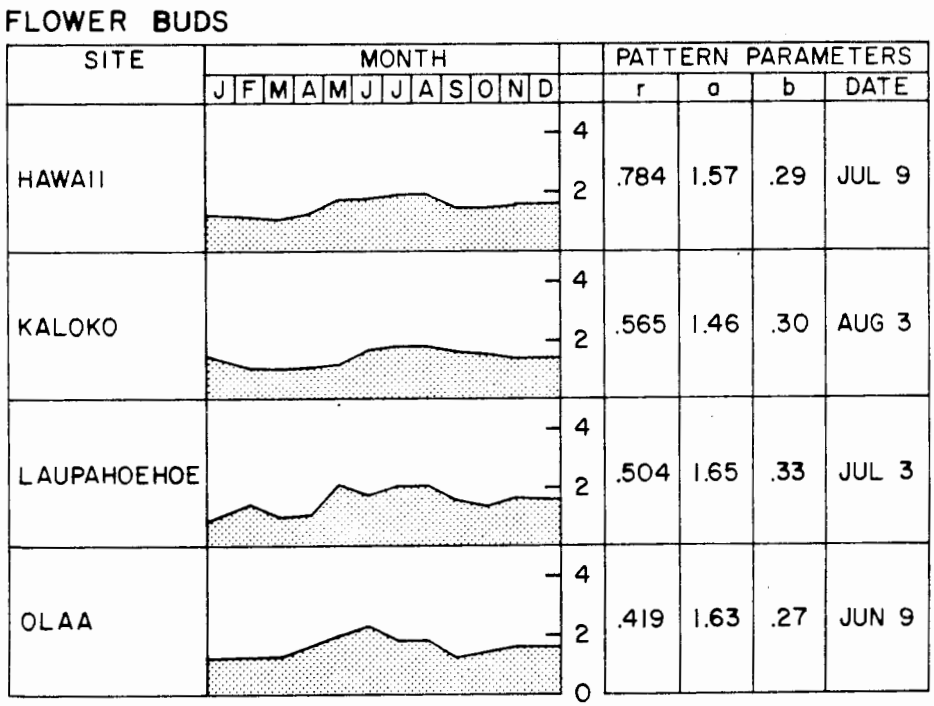


Fig. 15. Comparison of the seasonal changes in the magnitude of flowering (budding) in three populations of Passiflora mollissima on the island of Hawai'i with the mean response of all populations. Based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement or maximum value.

ANTHESIS

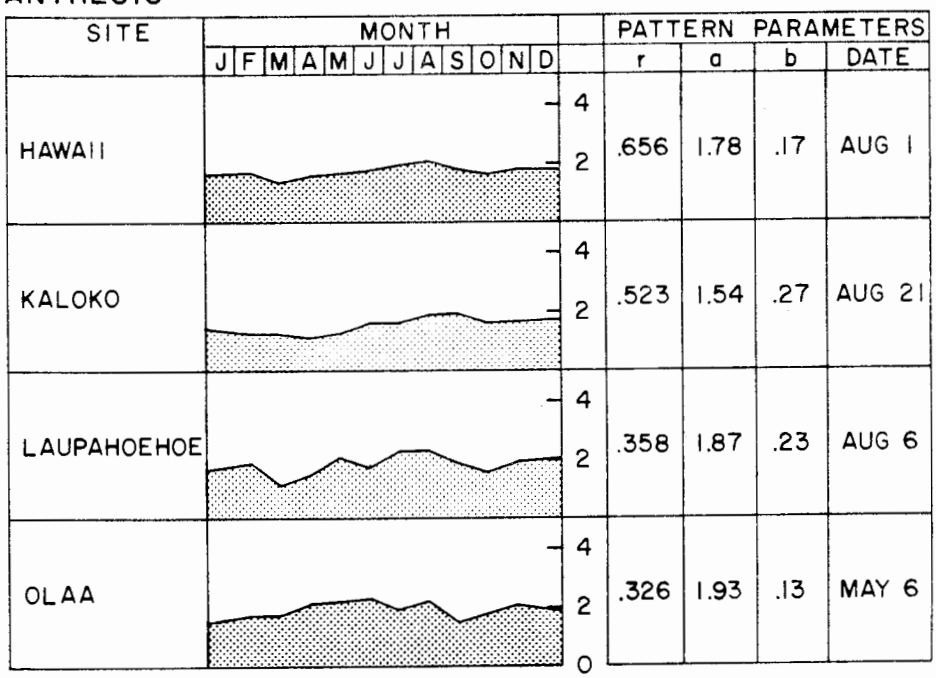


Fig. 16. Comparison of the seasonal changes in the magnitude of flowering (anthesis) in three populations of Passiflora mollissima on the island of Hawai'i with the mean response of all populations. Based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement or maximum value.

FRUITING

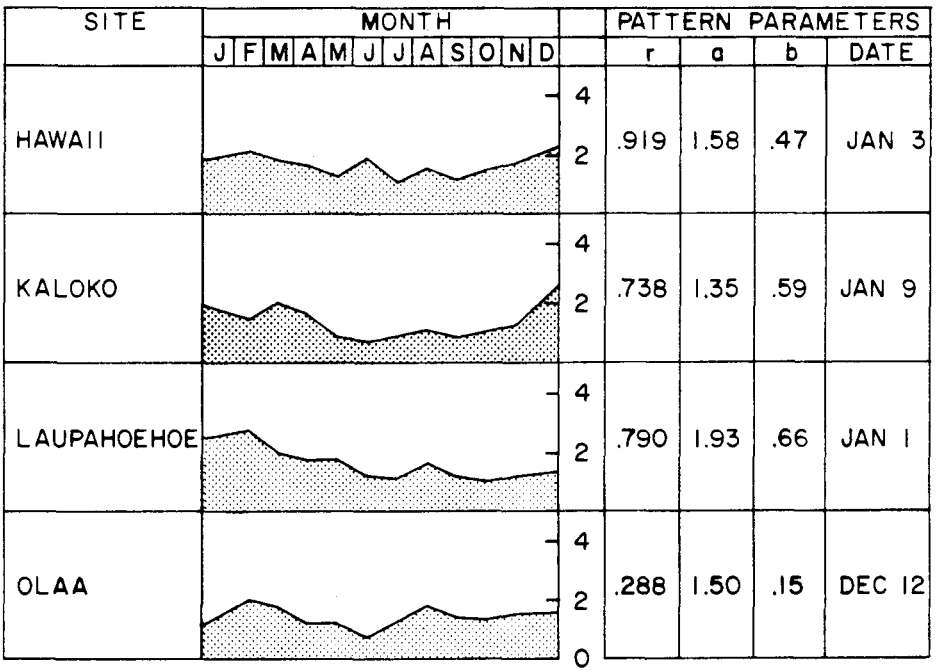


Fig. 17. Comparison of the seasonal changes in the magnitude of fruiting in three populations of Passiflora mollissima on the island of Hawai'i with the mean response of all populations. Based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement or maximum value.

FLUSHING

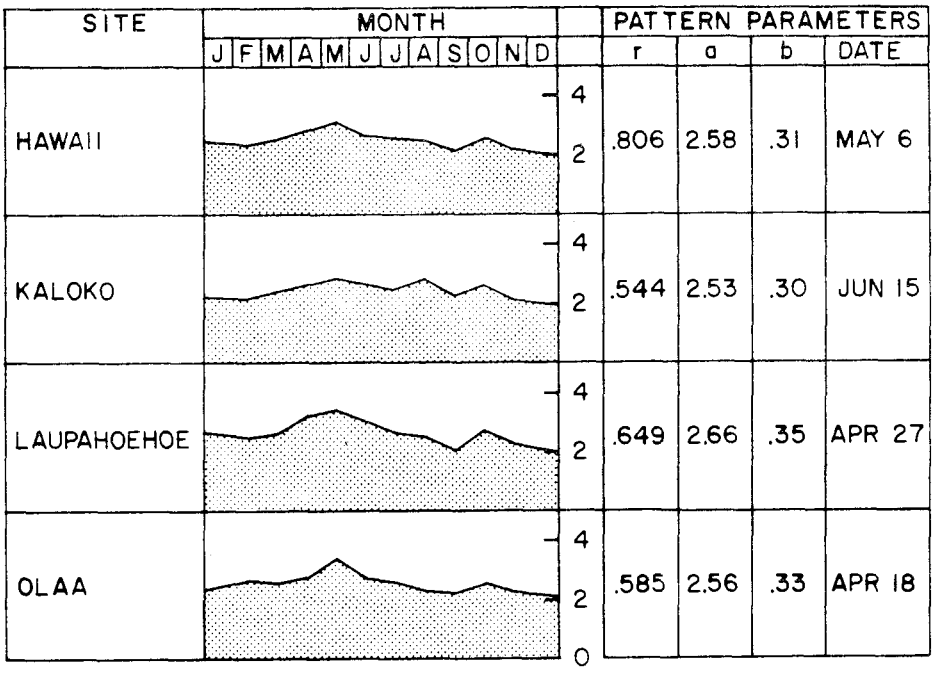


Fig. 18. Comparison of the seasonal changes in the magnitude of flushing in three populations of Passiflora mollissima on the island of Hawai'i with the mean response of all populations. Based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement or maximum value.

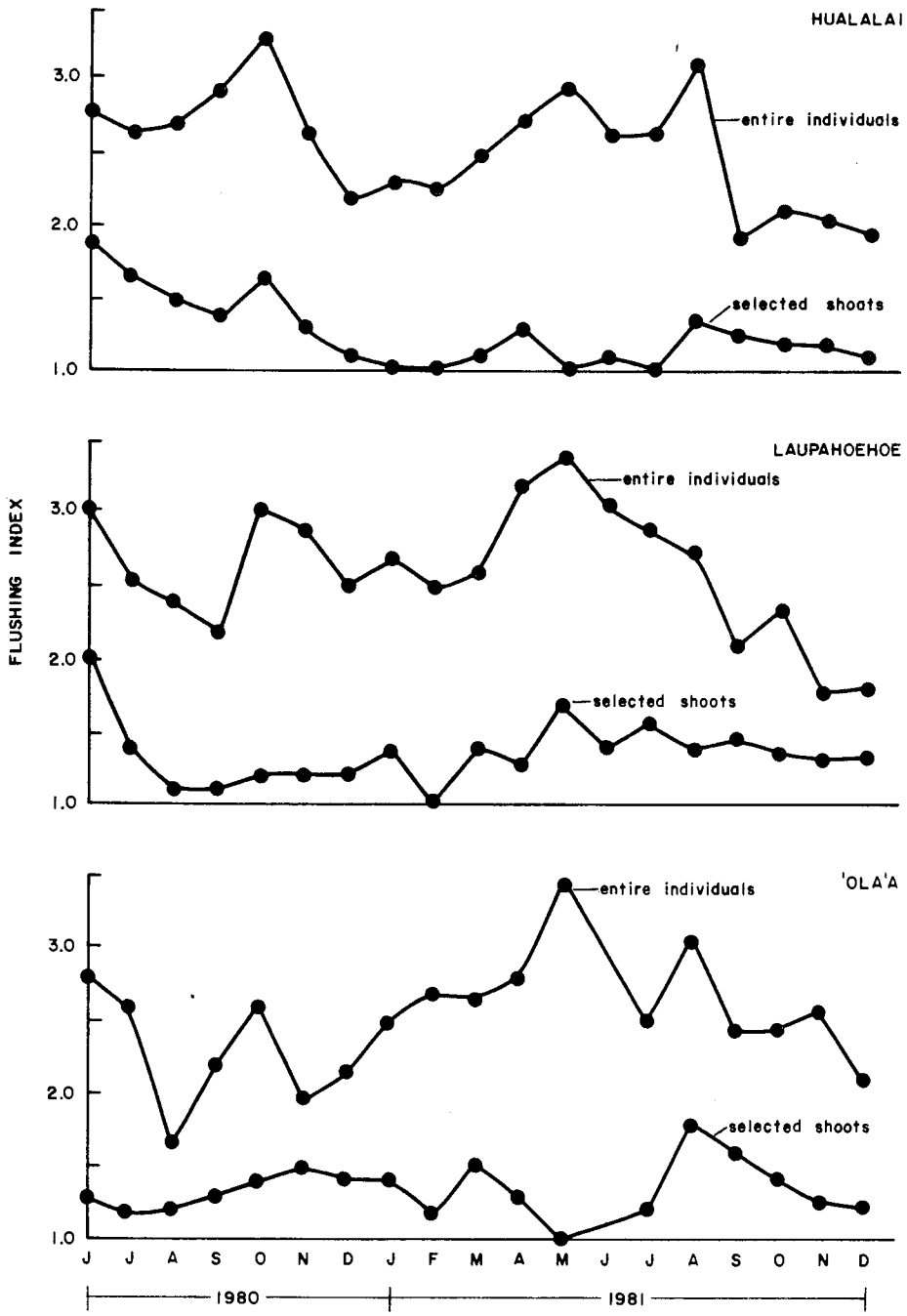


Fig. 19. Comparison of the relative magnitude and seasonality of flushing obtained by sampling entire individuals versus a selected shoot per individual.

GROWTH (length)

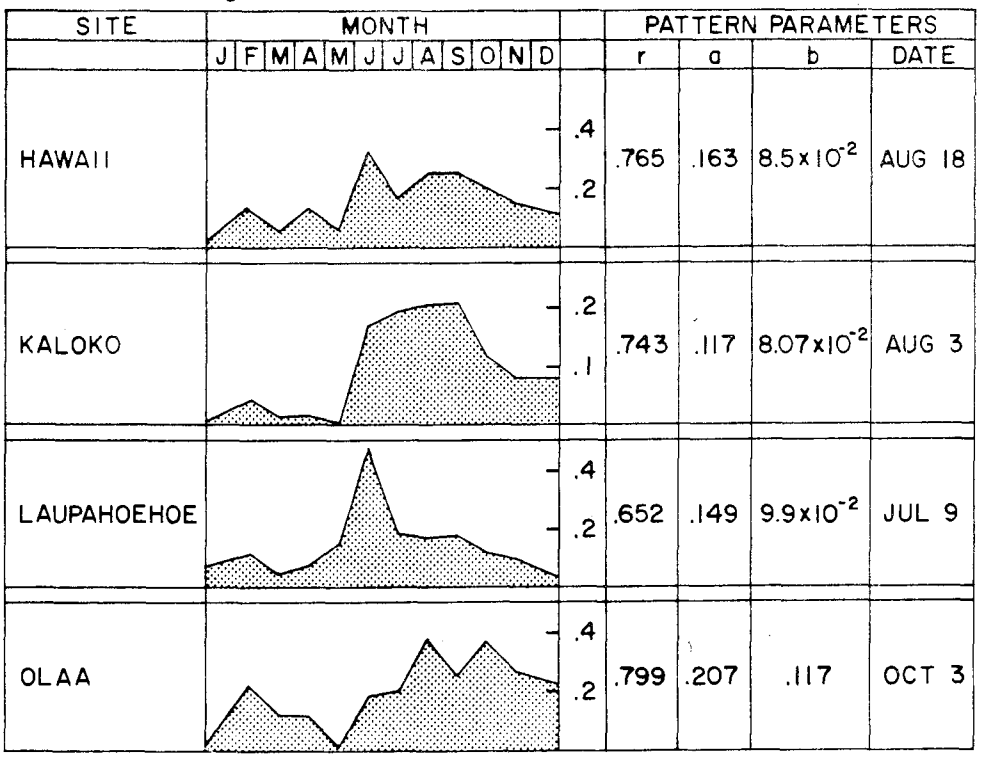


Fig. 20. Comparison of the seasonality in shoot growth (increase in shoot length cm/day) in three populations of Passiflora mollissima in the island of Hawai'i with the mean response of all populations. Based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement or maximum value.

GROWTH (diameter)

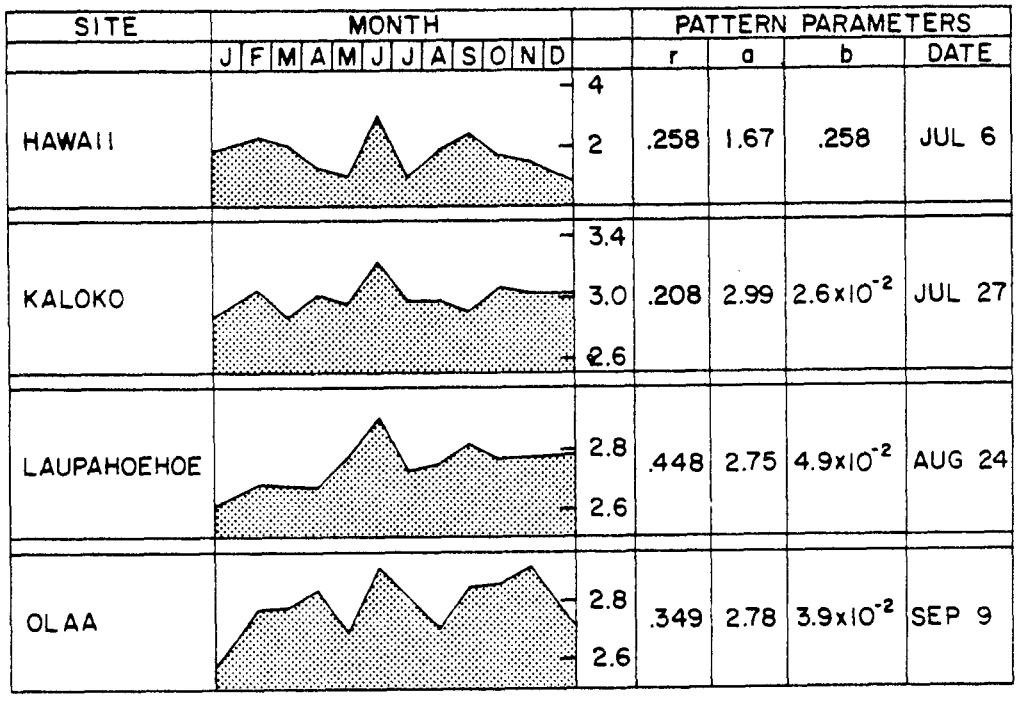


Fig. 21. Comparison of the seasonality in shoot growth (increase in shoot diameter mm/yr) in three populations of Passiflora mollissima on the island of Hawai'i with the mean response of all populations. Based on the sine function (Bridges et al. 1981). r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement oe maximum value.

LEAF TURNOVER

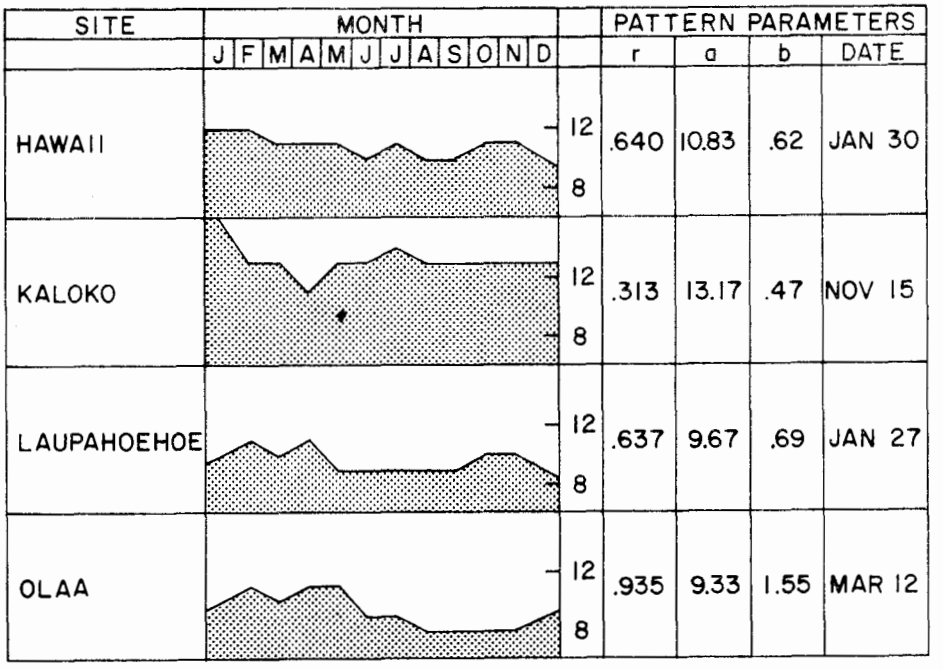
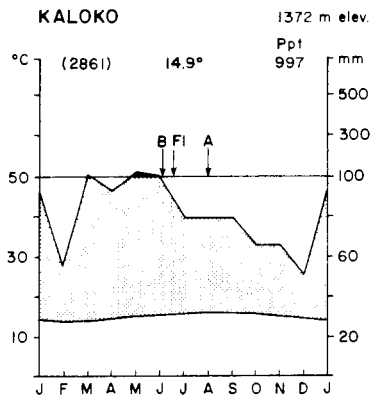
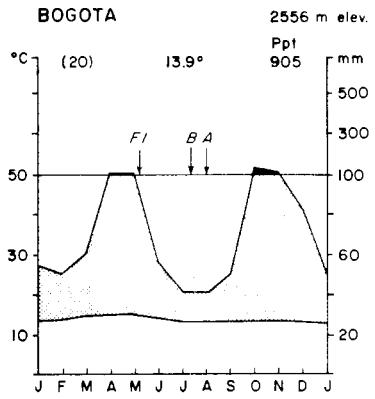


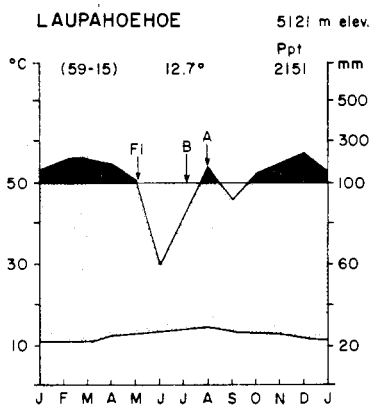
Fig. 22. Comparison of the seasonal changes in the magnitude of leaf turnover in three populations of Passiflora mollissima on the island of Hawai'i. Based on the sine function (Bridges et al. 1981): r = Pearson's correlation coefficient; a = monthly mean; b = annual amplitude; c = displacement or maximum value.

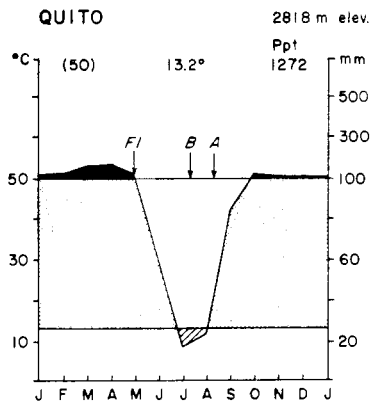
Fig. 23. Juvenile plant of Passiflora mollissima. Note distinctive morphology: sharply-lanceolate, deeply-lobed, thin leaves and long, flexible internodes and tendrils.

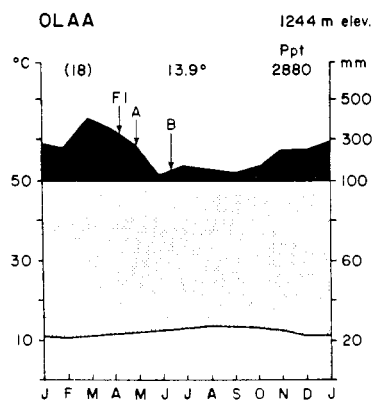
Fig. 24. Climate diagrams of the three phenology study areas in Hawai'i and three selected sites of Passiflora mollissima habitat in South America. Format follows Walter et al. (1975). Arrows indicate peak periods of flushing (Fl), budding (B) and anthesis (A) at each site in Hawai'i. The average value for each is plotted onto the South American sites. The uppermost line in each diagram represents mean monthly precipitation plotted with reference to the right-hand ordinate. The bottom line represents mean monthly air temperature plotted with reference to the left-hand ordinate. The mean annual precipitation at each site is found in the upper right-hand corner; the mean annual air temperature in the center. The figure in the upper left-hand corner represents the number of years of observations for temperature and rainfall (respectively), or both if only one number appears. Rainfall and temperature data for Hawai'i are from the nearest meteorological station; long-term averages from the State of Hawai'i (1970). South American data is from U. S. Dept. of Commerce (1959; 1966). Monthly rainfall values greater than 100 mm are indicated by blackened areas. Dotted areas represent "humid" periods; vertical hatching represents periods of drought.

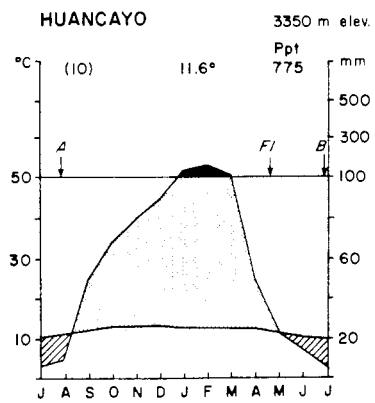

KALOKO
1372 m elev.
Ppt
997
mm
(2861)
14.9°
°C
B Fl A
500
300
100
60
50
30
20
10
J F M A M J J A S O N D J


BOGOTA
2556 m elev.
Ppt
905
mm
(20)
13.9°
°C
Fl B A
500
300
100
60
50
30
20
10
J F M A M J J A S O N D J


LAUPAHOEHOE
512! m elev.
Ppt
2151
mm
(59-15)
12.7°
°C
Fl B A
500
300
100
60
50
30
20
10
J F M A M J J A S O N D J


QUITO
2818 m elev.
Ppt
1272
mm
(50)
13.2°
°C
Fl B A
500
300
100
60
50
30
20
10
J F M A M J J A S O N D J


OLAA
1244 m elev.
Ppt
2880
mm
(18)
13.9°
°C
Fl A B
500
300
100
60
50
30
20
10
J F M A M J J A S O N D J


HUANCAYO
3350 m elev.
Ppt
775
mm
(10)
11.6°
°C
A Fl B
500
300
100
60
50
30
20
10
J A S O N D J F M A M J J

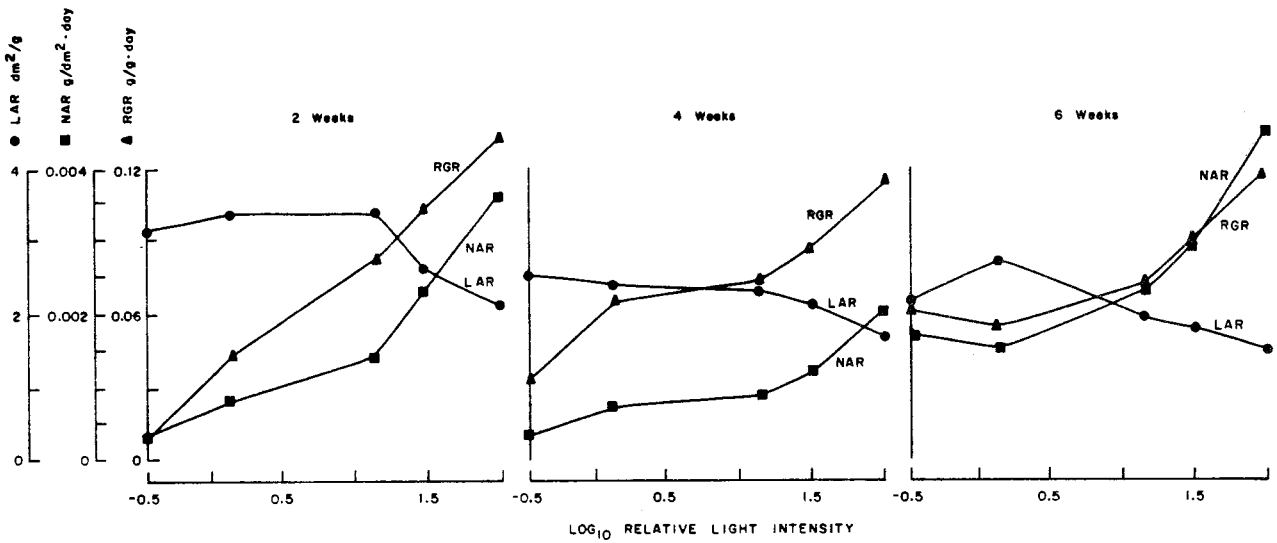


Fig. 25. Effects of varying light intensity on the relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) of Passiflora mollissima.

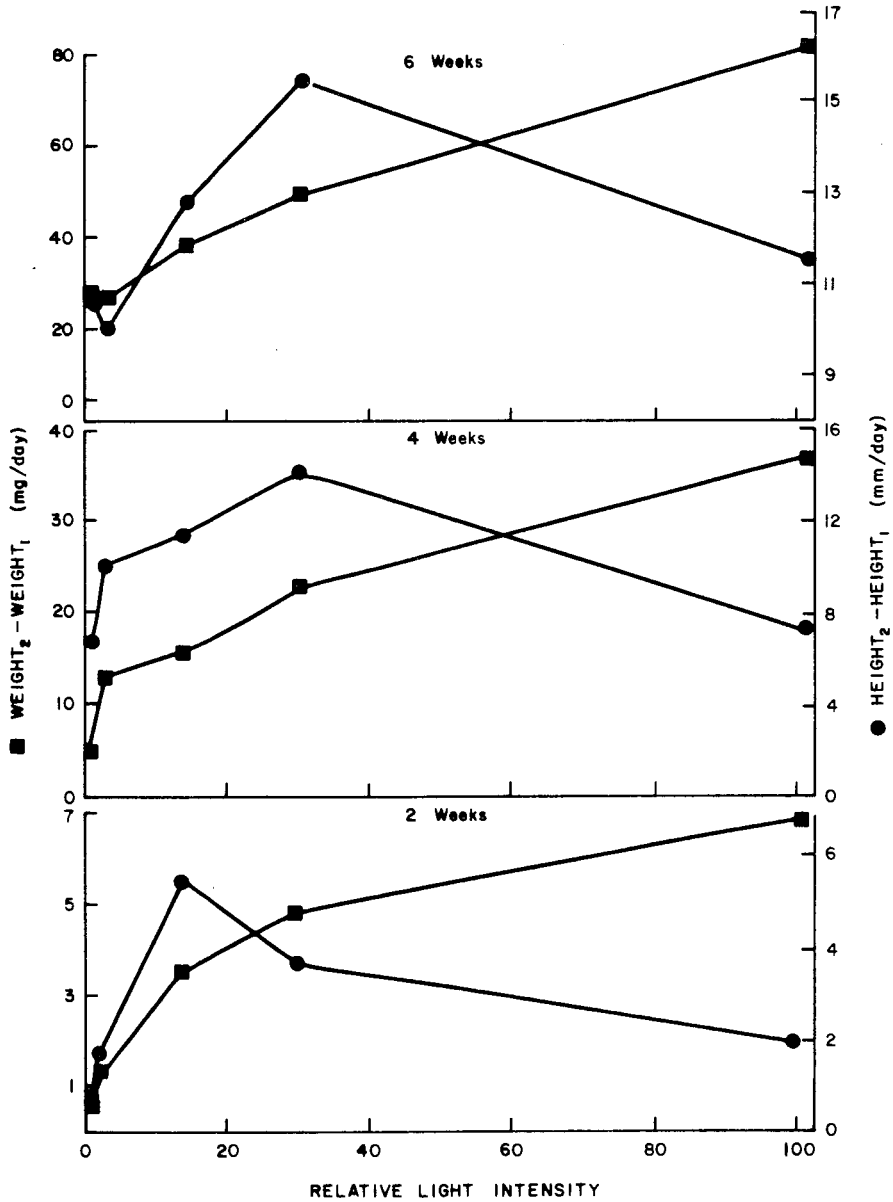


Fig. 26. Effects of varying light intensities on the height and weight of Passiflora mollissima.

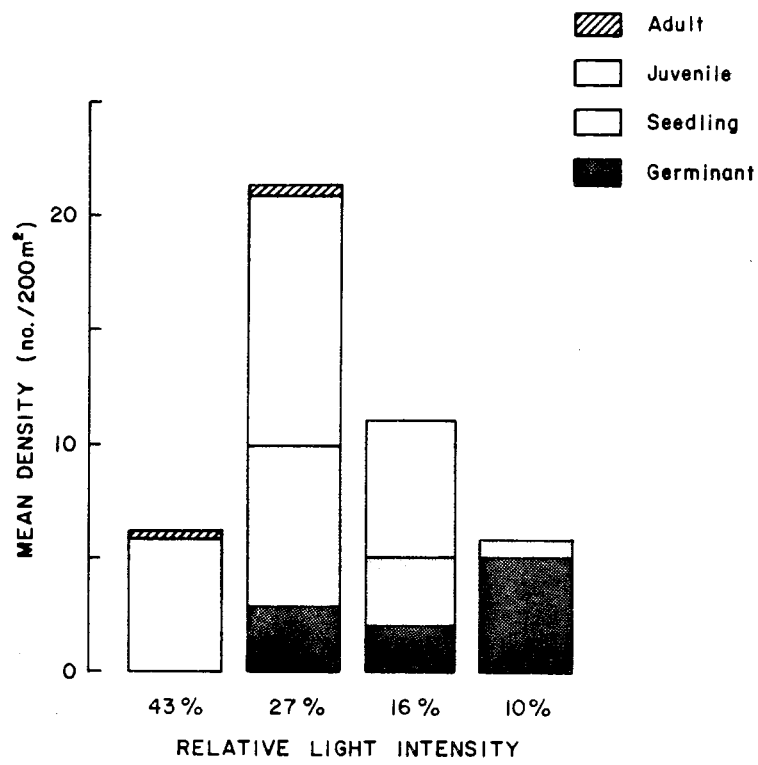


Fig. 27. Mean density (no./200 m^2) of Passiflora mollissima under various levels of relative irradience (RLI) associated with experimental canopy removal.

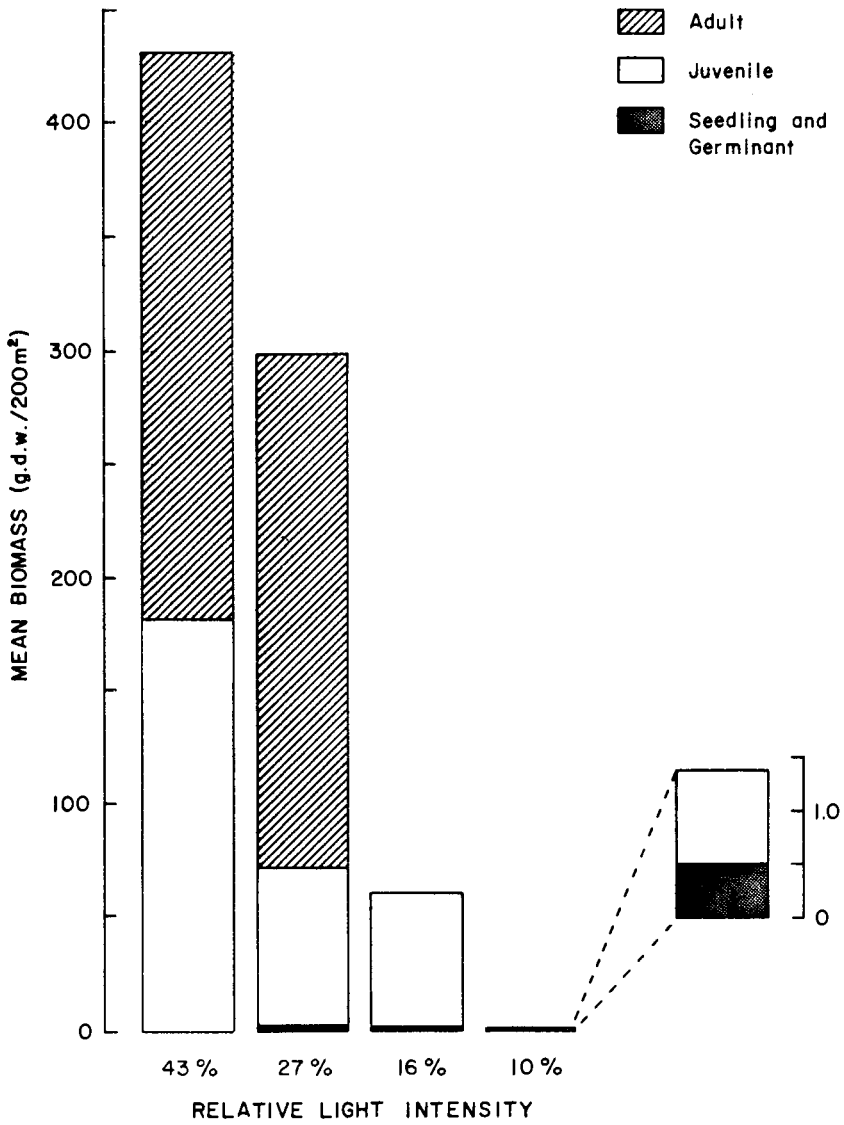


Fig. 28. Mean biomass (g/200 m^2 dry wt.) of Passiflora mollissima under various levels of relative irradiance (RLI) associated with experimental canopy removal.

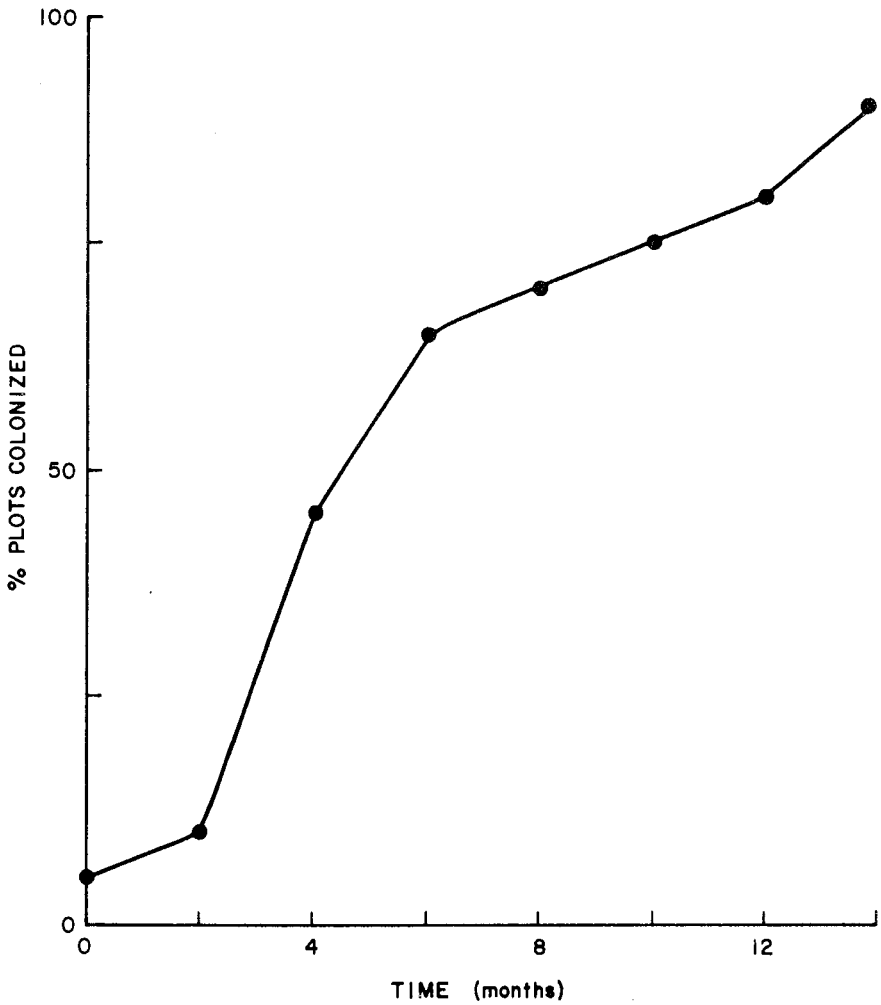


Fig. 29. Rate of colonization by Passiflora mollissima under conditions of artificial canopy removal.

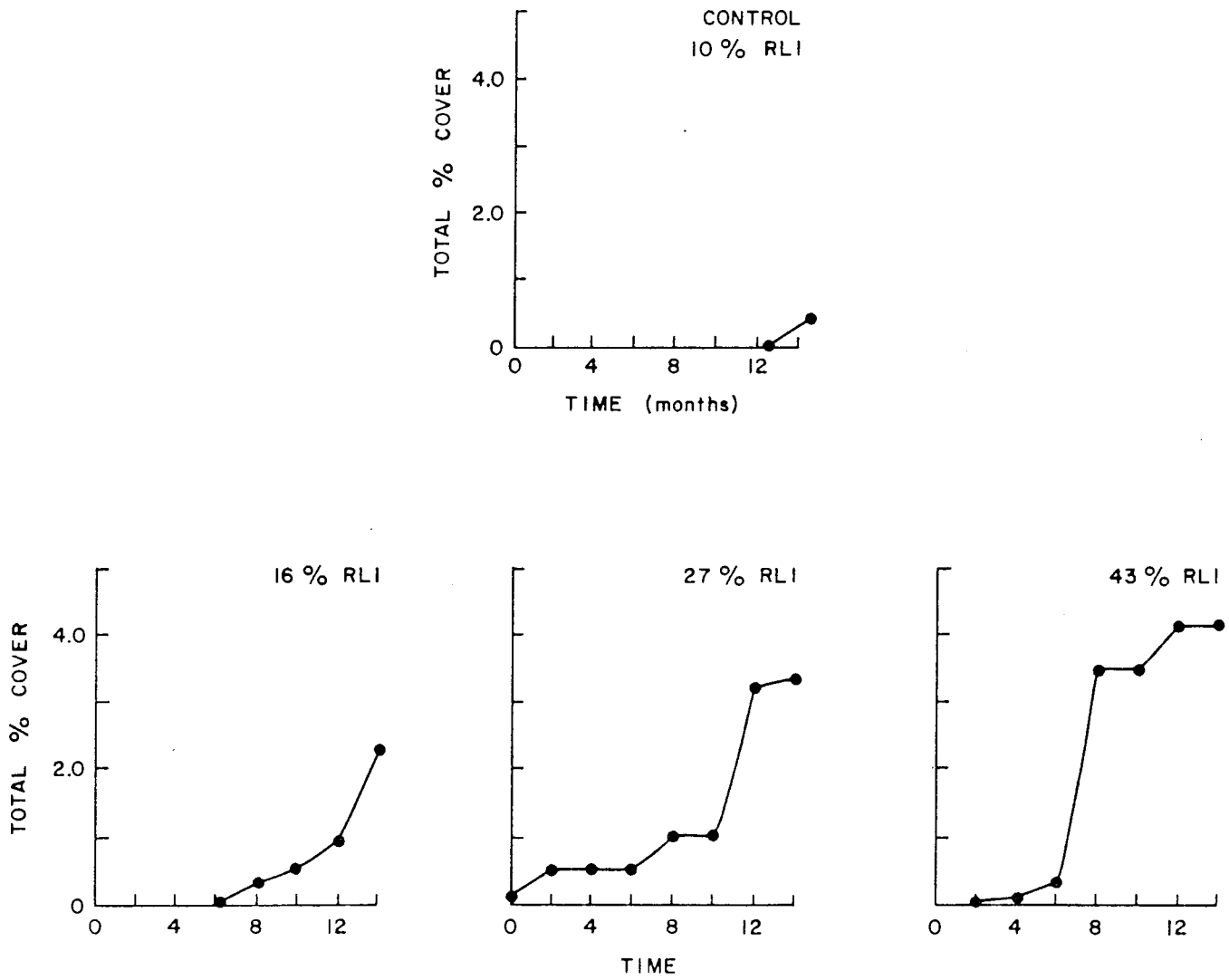


Fig. 30. Increase in total cover of Passiflora mollissima under various levels of relative irradiance (RLI) during 14 months of canopy disturbance.

APPENDIX 1: Count-plot Analysis of the Population Structure of *Passiflora mollissima*

Tables 20-26. Count-plot analysis of the population structure of *Passiflora mollissima* at seven selected sites on the island of Hawai'i. Raw data counts of density in 10 X 10 m contiguous plots. The reproductive classes were subsampled at several sites, as indicated.

Table 16. Count-plot analysis of the population structure of Passiflora mollissima at Kaloko-1. Raw data counts: enumeration in 10 x 10 m contiguous subplots. Total area of all plots 1000 m^2.

Basal diameter class (mm)	range (mm)	number of individuals
3	(1- 5)	16
8	(6-10)	22
13	(11-15)	33
18	(16-20)	32
23	(21-25)	12
28	(26-30)	1

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(<0.1)	182	500 m^2
2	(0.1-0.5)	215	500 m^2
3	(0.6-1.0)	31	1000 m^2

Table 17. Count plot analysis of the population structure of Passiflora mollissima at Kaloko-2. Raw data counts: enumeration in 10 x 10 m contiguous subplots. Total area of all plots 1000 m^2.

Basal diameter class (mm)	range (mm)	number of individuals
3	(1- 5)	23
8	(6-10)	54
13	(11-15)	33
18	(16-20)	23
23	(21-25)	22
28	(26-30)	1
33	(31-35)	2
38	(36-40)	0
43	(41-45)	0
48	(46-50)	1

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(< 0.1)	152	12.5 m^2
2	(0.1-0.5)	102	300 m^2
3	(0.6-1.0)	30	1000 m^2

Table 18. Count-plot analysis of the population structure of Passiflora mollissima at Laupehoehoe-1. Raw data counts: enumeration in 10 x 10 m contiguous subplots. Total area of all plots 1500 m^2.

Basal diameter class (mm)	range (mm)	number of individuals
3	(1 - 5)	17
8	(6-10)	21
13	(11-15)	4
18	(16-20)	5
23	(21-25)	0
28	(26-30)	2
33	(31-36)	1
38	(36-40)	4
43	(41-45)	2
48	(46-50)	1
53	(51-55)	1

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(< 0.1)	706	1500 m^2
2	(0.1-0.5)	51	1500 m^2
3	(0.6-1.0)	8	1500 m^2

Table 19. Count-plot analysis of the population structure of Passiflora mollissima at Laupahoehoe-2. Raw data counts: enumeration in 10 x 10 m contiguous subplots. Total area of all plots 1200 m^2.

Basal diameter class (mm)	range (mm)	number of individuals
3	(1- 5)	20
8	(6-10)	32
13	(11-15)	20
18	(16-20)	14
23	(21-25)	1
28	(26-30)	1
33	(31-35)	2
38	(36-40)	1
43	(41-45)	0
	(46-75)	0
78	(76-80)	1
83	(81-85)	1

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(<0.1)	1385	25 m^2
2	(0.1-0.5)	65	600 m^2
3	(0.6-1.0)	37	600 m^2

Table 20. Count-plot analysis of the population structure of Passiflora mollissima at Laupehoehoe-3. Raw data counts: enumeration in 10 x 10 m contiguous subplots. Total area of all plots 1200 m^2.

Basal diameter classes (mm)	range (mm)	number of individuals
3	(1- 5)	11
8	(6-10)	14
13	(11-15)	15
18	(16-20)	6
23	(21-25)	1
28	(26-30)	2
33	(31-35)	2
38	(36-40)	2
43	(41-45)	1
48	(46-50)	0
53	(51-55)	1

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(< 0.1)	221	8.25 m^2
2	(0.1-0.5)	64	1200 m^2
3	(0.6-1.0)	26	1200 m^2

Table 21. Count-plot analysis of the popualtion structure of Passiflora mollissima at 'Ola'a-1. Raw data counts: enumeration in 10 x 10 m contiguous cubplots. Total area of all plots 800 m^2.

Basal diameter classes (mm)	range (mm)	number of individuals
3	(1- 5)	22
8	(6-10)	11
13	(11-15)	6
18	(16-20)	0
23	(21-25)	0
28	(26-30)	0
33	(31-35)	0
38	(36-40)	0
43	(41-45)	0
48	(46-50)	1

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(< 0.1)	51	800 m^2
2	(0.1-0.5)	20	800 m^2
3	(0.6-1.0)	20	800 m^2

Table 22. Count-plot analysis of the population structure of Passiflora mollissima at 'Ola'a-2. Raw data counts: enumeration in 10 x 10 m contiguous subplots. Total area in plots 700 m^2.

Basal diameter classes (mm)	range (mm)	number of individuals
3	(1- 5)	24
8	(6-10)	11
13	(11-15)	0
18	(16-20)	5
23	(21-25)	4
28	(26-30)	1
33	(31-35)	1
38	(36-40)	3

Reproduction classes (ht)	range (cm)	number of individuals	total area sampled
1	(< 0.1)	207	700 m^2
2	(0.1-0.5)	60	700 m^2
3	(0.6-1.0)	24	700 m^2

APPENDIX 2: Climates of the Three Phenology Study Sites

Unusually-dry weather conditions prevailed during much of the phenological monitoring period (1980-1981). Following is a graphical comparison of the these years to the long-term averages at each of the three sites with the use of climate diagrams (Walter et al. 1975). The uppermost line in each diagram represents mean monthly precipitation plotted with reference to the right-hand ordinate. The bottom line represents mean monthly air temperature plotted with reference to the left-hand ordinate. The mean annual precipitation is found in the upper-right hand corner of each diagram; the mean annual air temperature in the center. The figure in the upper left represents the number of years of observations for temperature and rainfall (respectively) or both, if only one number appears. Rainfall and temperature data are from the nearest meteorological station; long-term averages from State of Hawai'i (1970). Monthly rainfall values greater than 100 mm are indicated by blackened areas. Dotted areas indicate periods of climatic drought; vertical hatching represents humid periods.

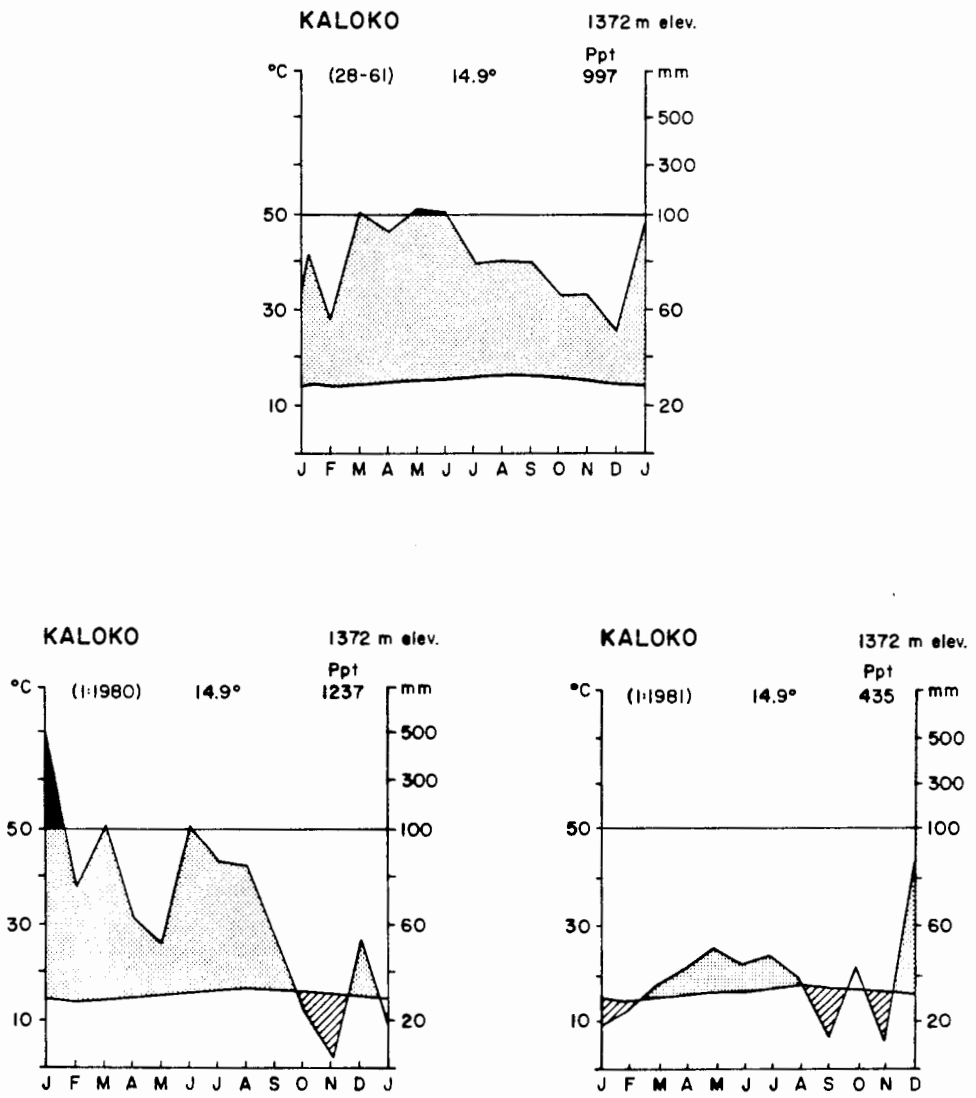


Fig. 31. Comparison of the long-term climate with the study years (1980-1981) at Kaloko, Hawai'i.

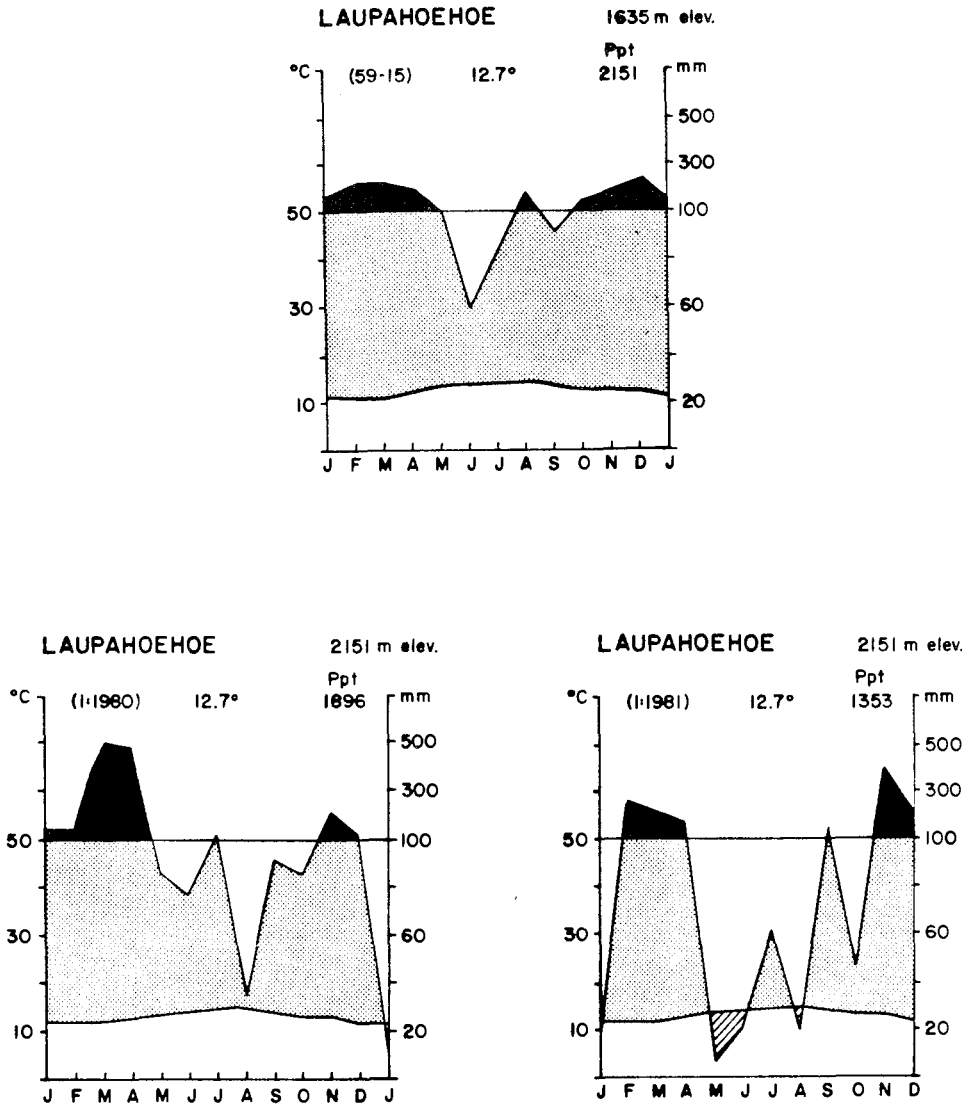


Fig. 32. Comparison of the long-term climate with the study years (1980-1981) at Laupahoehoe, Hawai'i.

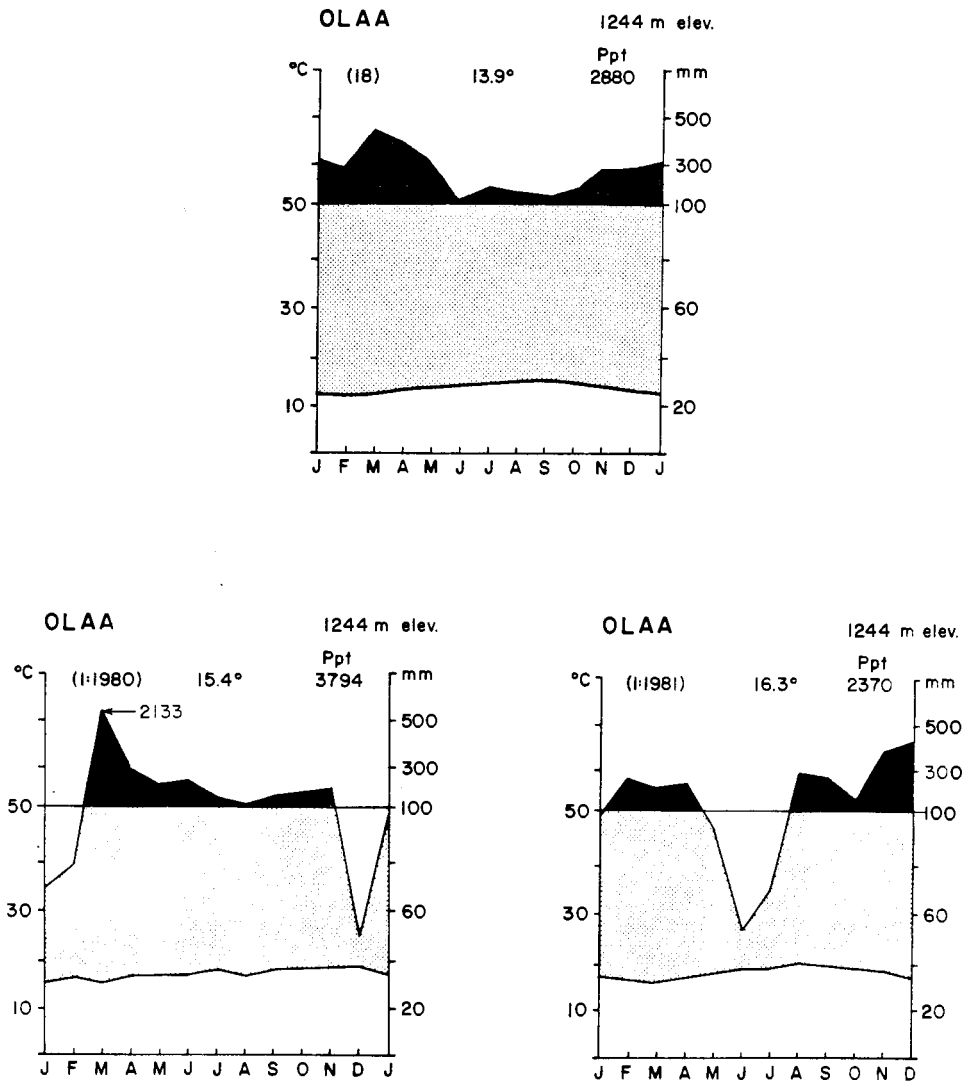


Fig. 33. Comparison of the long-term climate with the study years (1980-1981) at 'Ola'a, Hawai'i.

APPENDIX 3: Management Recommendations

Passiflora mollissima (banana poka) has invaded and is expanding in a wide range of habitats in Hawai'i. The successful pattern of resource allocation of this vine (rapid growth rates, early reproductive maturity, continuous reproduction and high seed output), combined with the lack of any serious predators or pathogens and effective dispersal by a host of exotic animals, has led to the rapid spread of populations in Hawai'i. Small scale, localized efforts at control or eradication P. mollissima are labor intensive and counter-productive in the long run. Certain small, isolated populations, such as the one found at Kula, Maui could be held in check, however. Large-scale, chemical control is undesirable due to its potentially deleterious effect on the native flora and fauna in the area. Biological control is currently the most feasible, effective means of large-scale control of this forest pest. A successful bio-control program is necessarily a long-term commitment and post-release studies are an integral part of any program.

In the meantime, the spread and proliferation of this weed should be limited through the control of feral animals and forest disturbance, where possible. Although P. mollissima is shade-tolerant through much of its life cycle, optimal growth and reproduction occurs in full sunlight. Practices which tend to open up the canopy, such as logging, hapu'u harvesting and large-scale clearing, should be avoided where P. mollissima is present, even in low densities. Manual control of small, expanding populations, following canopy-opening storms, in areas such as the 'Ola'a Tract may be possible and should be attempted on a trial basis, if manpower is available. It is evident from the study of the biology of this species that control of the banana poka is closely associated with the control of feral pigs and certain exotic birds. Pigs are the principal dispersal agent in most areas and their rooting activities often enhance seedling establishment. Certain birds with more limited distributions, such as the Kalij pheasant, may be controlled in areas where banana poka is present but more wide-ranging forest birds would be more difficult to control. Finally, the public must be educated regarding the problem that banana poka poses in our native forests. Its edible fruit and attractiveness as an ornamental could easily lead to its intentional spread to new areas, particularly by uninformed malihinis (newcomers), as has happened in the past.